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Unique foraging behaviours among sympatric stingrays in a reef-flat nursery

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ABSTRACT

Context. Intertidal reef flats serve as communal nurseries for juvenile rays, where they perform important functional roles. Although detailed assessments of foraging behaviours would provide critical insights into resource use and fine-scale trophic interactions among species, this has largely been unexplored. **Aims.** We compared the foraging behaviours of cowtail stingrays (*Pastinachus ater*), mangrove whiprays (*Urogymnus granulatus*) and pink whiprays (*Pateobatis fai*) at Pioneer Bay, Orpheus Island, to assess temporal foraging patterns and to compare species-specific resource use and functional roles. **Methods.** In 2021 and 2023, individual rays ($n = 96$) were followed within the intertidal reef flat for 7–18 min (mean = 13.5 min) by using aerial drones at heights of 3–5 m, and details were recorded on all foraging behaviours. **Key results.** *P. ater* and *U. granulatus* fed more frequently during low tidal heights, which decreased with rising tidal levels. Both *P. ater* and *P. fai* preferred foraging on smooth sand substrates and primarily used non-disruptive feeding behaviours. Species-specific foraging patterns were also observed, such that *P. ater* showed greater preferences for intense excavation and *U. granulatus* preferred feeding among coral rubble more than did other species. **Conclusions.** These species exhibited distinct foraging strategies that may enable resource partitioning, although overlap in other aspects of foraging and space use may also assist in maintaining functional redundancy within the reef flat nursery. **Implications.** Behavioural data provide meaningful insights on foraging mechanisms, particularly if results are interpreted alongside other methods in future research.

Keywords: behaviour, drones, ecological role, elasmobranch, feeding ecology, habitat use, intertidal, resource partitioning.

Introduction

Within marine communities, functionally similar species adopt various evolutionary strategies to reduce interspecific competition and facilitate coexistence (Ross 1986; Link and Auster 2013; Lear *et al.* 2021). Elasmobranch nurseries may be key areas that exemplify this dynamic, where high abundances within spatially restricted habitats may increase competition for limited resources (Kinney *et al.* 2011). In areas with high spatial overlap among sympatric competitors, resource partitioning is often indicated by dietary differentiation and distinct trophic niches (Yick *et al.* 2011; Pardo *et al.* 2015; Mulas *et al.* 2019; Elston *et al.* 2020). Additional mechanisms include foraging at different times (Bass *et al.* 2021; Hayata *et al.* 2021; Lear *et al.* 2021) or exhibiting spatial preferences by depth, substrate or proximity to specific habitat features (e.g. mangrove edges) (White and Potter 2004; Ajemian and Powers 2016). Although complex in nature, these examples demonstrate how species exploit available resources on the basis of their unique competitive abilities, which could be driven by factors related to jaw morphology (Dean *et al.* 2007; Pardo *et al.* 2015; Kolmann *et al.* 2023) or body size (Scharf *et al.* 2000; Barbini *et al.* 2018; Weideli *et al.* 2023).

Rays in intertidal zones function as mesopredators and ecosystem engineers, which are capable of significantly shaping ecosystem dynamics through their feeding behaviours (Flowers *et al.* 2021). Ray bioturbation contributes to several physical processes such as sediment turnover (Meysman *et al.* 2006; Grew *et al.* 2025) and nutrient cycling (Valentine *et al.* 1994; O'Shea *et al.* 2012; Takeuchi and Tamaki 2014), which can further create foraging opportunities for other benthic predators (Boaden and Kingsford 2012; Kiszka *et al.* 2015). Ray feeding pits can also drastically transform the geomorphology of soft-bottom substrates over time, particularly when feeding occurs consistently within concentrated areas or habitats (Cross and Curran 2000; Giaroli *et al.* 2024; Nauta *et al.* 2024). Therefore, understanding the drivers of foraging habitat selection is essential for assessing the ecological impacts and services of rays within intertidal ecosystems. Where multiple ray species coexist, their contributions to ecosystem processes are likely to vary over fine spatial scales because of differences in habitat use and foraging behaviours among sympatric species and life stages. For example, if one ray species habitually feeds along the top layers of sediment, it is likely to turn over less sediments over time than is another species that consistently excavates the substrate to extract deeper-buried prey (Kyne and Bennett 2002; Beckman 2017; Tamaki *et al.* 2021). Moreover, where one species feeds over larger spatial areas than does another, this may also influence their participation in trophic interactions and broader ecosystem connectivity (Ajemian and Powers 2014; Sheaves *et al.* 2024).

Although knowledge of ray feeding ecology is generally derived from trophic studies (Elston *et al.* 2020; Martins *et al.* 2022; Queiroz *et al.* 2023), behavioural observations provide further insights into fine-scale habitat use. Various aspects of ray behaviour, such as aggregation patterns, swimming, resting and feeding have been investigated using multiple methods, including stationary cameras (Kanno *et al.* 2019), boat surveys (Vaudo and Heithaus 2009) and snorkel surveys (Semeniuk and Dill 2005, 2006). In recent years, behaviours of rays have also been documented in shallow waters or along the surface by using aerial drone surveillance (Frixione *et al.* 2020; Oleksyn *et al.* 2021*a*; Crook *et al.* 2022). Unlike other methods that rely on instantaneous observations or rays remaining in the camera field of view, drones can follow individual rays with minimal disturbance to their natural states (Bourke *et al.* 2023) while collecting high-resolution behavioural data over prolonged time frames. Despite the advances in drone technology, very few studies have provided detailed accounts of ray foraging behaviours (Oleksyn *et al.* 2021*a*). A previous study that compared foraging behaviours between Australian whiprays (*Himantura australis*) and cowtail stingrays (*Pastinachus ater*) showed how each species foraged over different spatial areas and consistently used different foraging strategies (Crook *et al.* 2022), suggesting a reliance on different prey and complementary functional roles in intertidal sand flats. Overall, more comparative behavioural studies are needed to bridge the gaps between dietary habits, fine-scale habitat selection and foraging mechanisms, as well as understanding the effects of species-level contributions to ecosystem processes.

Pioneer Bay, Orpheus Island, is a year-round nursery for juvenile rays (Martins 2019). Three species are common on the reef flat, including the broad cowtail stingray (*P. ater*), mangrove whipray (*Urogymnus granulatus*) and pink whipray (*Pateobatis fai*). Previous studies at this location have reported trophic niche separation between *U. granulatus* and *P. ater* (Martins *et al.* 2022), as well as differences in fine-scale habitat use within the reef flat (Kanno *et al.* 2019). Across other nearshore contexts, dietary studies have shown that *U. granulatus* primarily consumes decapod crustaceans, whereas *P. ater* targets a range of bivalves, crustaceans and annelids (Crook 2020; Elston *et al.* 2020; Martins *et al.* 2022). Consequently, the vertical depth at which each species extracts their preferred prey from the sediment column could have differential impacts on pit formation and subsequent bioturbation outputs. Whereas these findings provide compelling evidence of inter-specific resource partitioning, behavioural mechanisms underlying the foraging habits of each species remain unexplored. Moreover, with an absence of trophic studies on *P. fai* at this location, their potential interactions with other species remain speculative. In this study, we compared the foraging behaviours among these three sympatric ray species at Pioneer Bay, Orpheus Island, to assess temporal foraging patterns and whether behavioural distinctions supported species-specific resource partitioning and functional roles.

Materials and methods

Study site

Pioneer Bay is a 400-m-wide intertidal reef flat located on the western side of Orpheus Island in the northern Great Barrier Reef (Fig. 1). The site experiences semi-diurnal tidal cycles. The tidal flat is mostly unvegetated, except for patches of mangroves that grow along the shoreline edges and some growths of macroalgae. Substrates include a mix of smooth sand and rubbly sand on the inner flat, which transitions to more rubbly sand and coral rubble on the outer flat and extending towards the reef crest (~350 m from the beach). Further details of the Pioneer Bay site have been provided by previous studies (Kanno *et al.* 2019; Martins *et al.* 2020, 2021; Higgins *et al.* 2024).

Video collection and analysis

Drone behaviour tracks of rays were collected during two visits to Pioneer Bay in 2021 and 2023. Data from 2021 were collected from 22 to 24 November, at the start of the tropical wet season, whereas data from 2023 were collected from 8 to 12 March, during the late wet season. Tidal ranges were similar between years (ranging from 0.9 to 2.6 m in 2021 and from 1.2 to 3.3 m in 2023 during the daytime low–high cycle), indicating similar patterns of tidal submergence. For the 2021 dataset, videos were collected only during the rising tide progressions during the morning hours (05:30–10:30 hours), whereas in 2023, tracks encompassed low, rising and high tides, which occurred during the morning and afternoon hours (07:00–17:30 hours). No tracks were collected during ebb tides for either year.

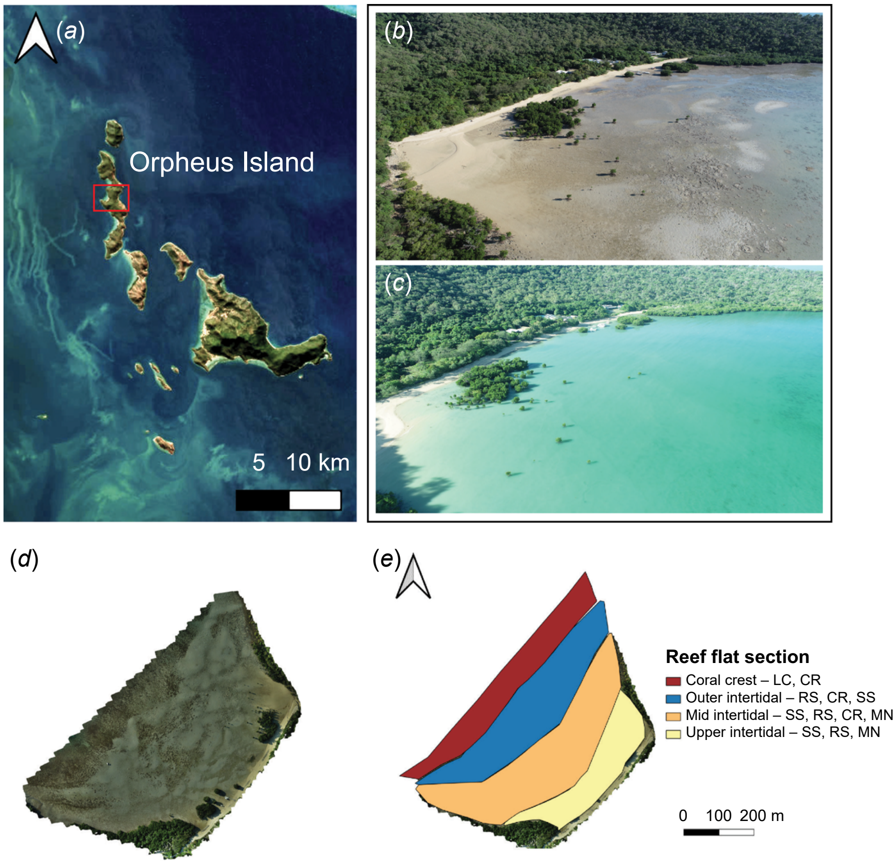

Fig. 1. Map showing the location of Pioneer Bay on the western side of Orpheus Island, North Queensland (*a*). The inset images show south-facing aerial overviews of the intertidal flat at tidal heights of (*b*) 1.5 m and (*c*) 2.5 m. Bottom panels show drone orthomosaic imagery of Pioneer Bay at low tide (*d*, *e*). Coloured polygons denote different foraging areas, which were modified from habitat sections described by Martins *et al.* (2020) and classified on the basis of both tidal exposure and habitat composition. CR, coral rubble; LC, live coral; MN, mangrove; RS, rubbly sand; SS, smooth sand.

Individual rays were tracked with a Phantom 4 Pro quadricopter drone (DJI, Shenzhen, PR China) operated by an on-ground pilot, following methods by Crook *et al.* (2022). Drone surveys were conducted in accordance with the Memorandum of Understanding between James Cook University and the Great Barrier Reef Marine Park (authorisation number CSE163). Flights were conducted during suitable visibility conditions, namely, during daylight hours, winds speeds of <25 km h^{-1}, no rainfall and tidal height readings at the Lucinda Offshore station of <3.0 m. Rays were generally tracked in depths of <1 m, although this could extend to 2 m where visibility allowed it. To start each behaviour track, the drone was launched and flown haphazardly at a height of 15–20 m until a ray was located. The drone was then lowered to a height of 3–5 m, which has been shown to have little effect on natural behaviour (Bourke *et al.* 2023). Video recording began once the focal ray was centred in the field of view, and this was maintained for the duration of the track. Data were not collected for other rays that passed through the field of view. Tracks were terminated once the drone battery dropped below 20% or the target ray was lost from view. Video track length was recorded, because this varied depending on the drone battery level when a ray was located and weather conditions (particularly wind) that affected battery life. For subsequent tracks, efforts were taken to direct the search away from the final position of the previous tracked ray.

Tracks were assigned one of the following three tidal-height categories, based on predicted tidal heights at the Lucinda Offshore station at the time of the flight: low (0.1–1.5 m), mid (1.6–2.2 m) and high (>2.2 m). During 'low' tidal heights, habitats adjacent to the beach and mangrove edges are mostly dry or shallowly inundated extending to the coral crest (~300–350 m from the beach). During 'mid' height ranges, nearly the whole flat is submerged up to the beach and mangrove edges, and at 'high' tidal heights, these areas are inundated in deeper water.

Data were then extracted for all feeding events per video track. Foraging commenced once a ray ceased forward swimming movement or moved backward to hover over a spot of interest before initiating foraging. First, the GPS coordinates of each event were recorded using the position of the drone at the onset of foraging as a proxy. Four foraging types were recognised, as defined by Crook *et al.* (2022). *Suction* was when a ray remained stationary, flattening its disc against the substrate and ejecting sediment through the spiracles. When *water jetting*, a ray remained stationary while emanating sediment plumes from all sides of the disc. *Excavation* was when a ray fed intensely with the rostrum and pectoral fins to displace sediment from the anterior and lateral disc margins. Last, *surface feeding* was when a ray foraged along the top of the sediment and created minimal sediment disturbance. If more than one behaviour was observed, the most prominent type was recorded.

Substrates where feeding occurred were classified into three main categories (Fig. 2). Feeding events were assigned to 'smooth sand' where there was little or no coral rubble present in the video frame and 'rubbly sand' if a ray foraged on sand that was interspersed with coral rubble (~50% of video frame). 'Coral rubble' was assigned when a ray fed directly on fragments of dead coral, either over a bottom of solid rubble or in rubbly sand patches. In the initial video analysis, a further classification of 'mangrove' was used for all feeding events that occurred within 1 m of the mangrove roots. However, the 'mangrove' classification was later excluded from analysis, because rays showed little foraging activity along mangrove edges. Moreover, potential feeding events were either difficult or impossible to observe from overhead if the ray was obstructed by the mangrove roots.

A feeding event was considered terminated once the ray moved away before foraging again or ceased foraging activities for >10 s. If a ray recommenced feeding <0.5 m from where the first feeding attempt occurred without switching foraging types or substrate, this was considered a continuation of the same feeding event. Total duration (s) was calculated from the start and end time of each feeding event and was not recorded if a feeding event had already commenced at the start of a track or if foraging continued after tracking concluded. For all feeding that occurred on smooth sand or rubbly sand substrates, it was documented whether an event created a feeding pit. Although surface feeding does not result in true pit formation, shallow feeding scars were also included, because these still represented some visible degree of disturbance. If the substrate was obscured by displaced sediments or this could not be confidently assumed by the intensity of the foraging event, pit or scar formation was omitted.

Statistical analysis

All statistical analyses were run using *R* (ver. 4.2.2, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/) with statistical significance assessed at $\alpha = 0.05$. Residual diagnostics for all models were evaluated using the packages *DHARMa* (ver. 0.4.6, see https://CRAN.R-project.org/package=DHARMa) and *performance* (ver. 0.10.2, see https://CRAN.R-project.org/package=performance; Lüdecke *et al.* 2021).

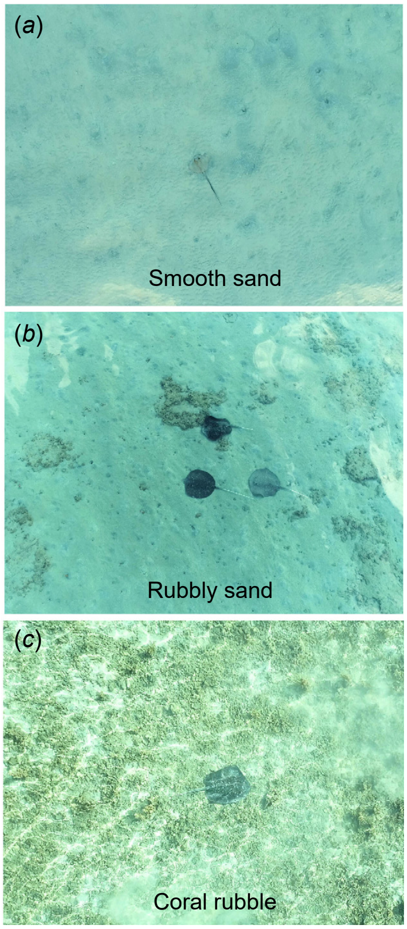

Fig. 2. Feeding events were assigned one of three substrate types. (*a*) Smooth sand (shown with one cowtail stingray, *Pastinachus ater*) was assigned where there was very little or no coral rubble. (*b*) Rubbly sand (shown with three mangrove whiprays, *Urogymnus granulatus*) included sandy patches that were interspersed with coral rubble fragments (~50% of video frame), but where feeding did not occur directly on the coral rubble. (*c*) Coral rubble (shown with one *U. granulatus*) was assigned when an event occurred directly on a fragment of coral, either on solid coral bottom or rubbly sand.

Effect of tide on ray foraging activity

Foraging activity was summarised using the following two metrics: *foraging rate* = number of independent feeding events per track standardised to 1 h; and *proportion of time foraging per track* = total seconds of ray foraging divided by total seconds engaged in other behaviours (swimming or resting). Owing to variable tracking times, a linear regression was applied (Gaussian distribution) to identify the relationships between foraging rate and track length, with year retained as a factor. For proportion of time foraging per track, a beta-regression model was run by using the *glmmTMB* package (ver. 1.1.5, see https://CRAN.R-project.org/package=glmmTMB; Brooks *et al.* 2017) because of the bounded nature of proportional data (values constrained between 0 and 1). Prior to analysis, a transformation of 0.001 was applied any proportions of zero (where no foraging occurred). For both response variables, additive models were compared against interaction models. In both cases, the additive models were selected as the most parsimonious.

Temporal patterns in foraging metrics were compared among species by tidal-height category (low, mid and high), and year (2021 *v.* 2023 datasets). Prior to analysis, statistical outliers within each species × tidal-height combination were identified on the basis of the interquartile ranges (values exceeding 1.5 × IQR above Q3 or below Q1). Although these extreme values provide insights into individual behavioural variability, they were removed ($n = 3$ for foraging rate, $n = 2$ for proportion of time foraging per track) to more effectively generalise species-level patterns. Models were constructed for each response variable (foraging rate and proportion of time foraging) by using the same family distributions as in the prior models testing effects of track length. Results were interpreted on the basis of additive models. The significance of each variable was evaluated using the 'Anova' function in the *car* package (ver. 3.1-1, see https://CRAN.R-project.org/package=car; Fox and Weisberg 2019). The predicted marginal means and pairwise contrasts were generated using the *emmeans* package (ver. 1.7.2, see https://CRAN.R-project.org/package=emmeans). For the proportion of time foraging, contrasts were interpreted using the odds ratios and back-transformed to the response scale for interpretation. All means were reported with ±1 s.e.

Foraging preferences among ray species

To examine whether there were significant associations between foraging type and substrate, the frequencies of feeding events for each substrate and foraging type were summarised across all three species. A Chi-Square test of variable independence was then applied ($\alpha = 0.05$), with values >2 indicating associations that deviated substantially from the expected frequencies. Residuals were then interpreted to identify the direction (positive or negative) and strength (distance from zero) for each combination. Foraging type *water jetting* was excluded from this analysis, because of a low number of overall observations (<1%).

Substrate and foraging type selections were compared among species by using multinomial logistic regression with a logit link function in the *mclogit* package (ver. 0.9.6, see https://CRAN.R-project.org/package=mclogit). This model structure was chosen because it could examine the effects of each fixed factor on a categorical response variable (species identity), while accounting for the non-independence of multiple feeding events within individual tracks. Prior to analysis, data were filtered to remove incomplete observations and rare event categories that would compromise model convergence (e.g. water jetting = <1% of all observations for foraging type). The estimated marginal means were used to estimate the probability of each species selecting each factor level (substrate = coral rubble, rubbly sand or smooth sand; foraging type = surface, excavation, suction). For *post hoc* analysis within *emmeans*, significance values were adjusted for multiple comparisons by using the Tukey method.

The likelihood of pit or scar formation was compared among species by using a generalised linear mixed model with a binomial distribution and logit link function, with track identity as a random effect. Only feeding events on smooth sand or rubbly sand substrates were analysed, because pits could not be formed on coral rubble. Mean probabilities from the *emmeans* package were interpreted using the odds ratios and converted to percentages ±1 s.e. for interpretation.

Results

Drone track summary

In total, 96 tracks were collected across two site visits in 2021 ($n = 44$) and 2023 ($n = 52$), of which 89 contained at least one feeding event (see Supplementary Table S1). Sampling efforts were similar for *P. ater* ($n = 40$; 9.2 h of tracking time) and *U. granulatus* ($n = 39$; 8.9 h), being the lowest for *P. fai* ($n = 17$; 4.4 h). Most tracks were collected during mid-tidal heights ($n = 42$; 8.8 h), which contained 340 feeding events (all from rising-tide periods). There were 37 tracks for low tidal heights (10.6 h), which contained 318 feeding events (265 during low tide, 83 during rising tides). Track representation was lowest for the high height range ($n = 17$; 3.8 h), with only 34 feeding events being recorded (all from rising tides). Track length ranged from 4.4 to 21.4 min, with a mean of 13.7 ± 0.4 s.e. min. Total foraging events per track ranged from 0 to 28 (mean = 7.0 ± 0.6 s.e. events).

In total, 312 feeding events were recorded for *P. ater*, 168 for *P. fai* and 212 for *U. granulatus*. The distribution of feeding events varied across the reef flat because of differences in path trajectories, which was inherently determined by tidal habitat availability at the time of each flight (Fig. 3). Most tracks were completed on the north-eastern side of the bay on the outer, middle and inner flat near the shoreline and mangroves, which created feeding event clusters within the bay.

Distributions of feeding durations varied broadly among species and foraging types (Fig. 4). Longest feeding durations were recorded for *P. ater* (median = 0.67 min), compared with *U. granulatus* (0.32 min) and *P. fai* (0.22 min) (Table 1). By foraging type, excavation was associated with the longest feeding times (median = 0.81 min). Both suction or surface feeding had similar feeding durations (0.26 and 0.27 min respectively). For water jetting, durations were highly variable because of the small sample size ($n = 13$) (Table 1).

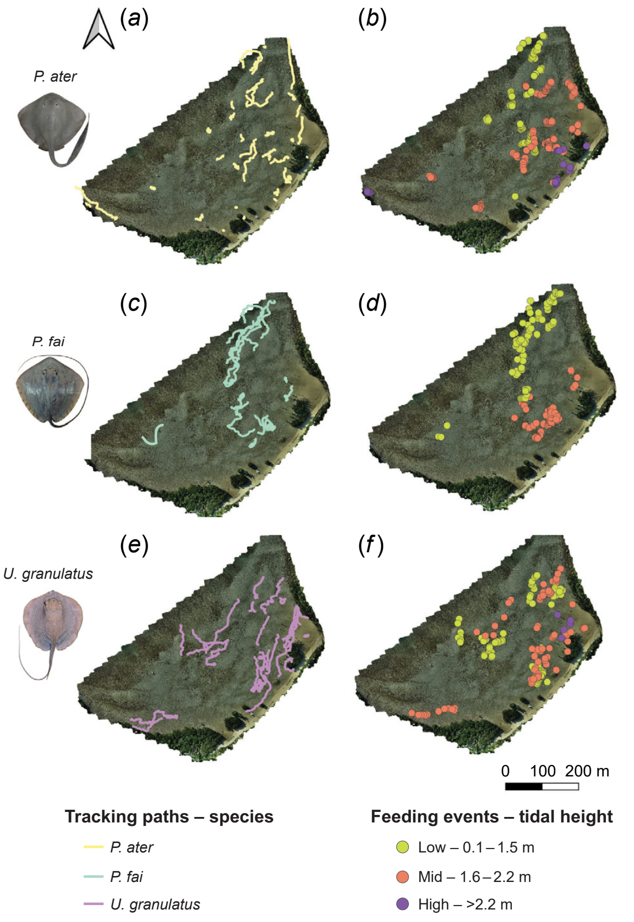

Fig. 3. Drone transect paths (left) and the point locations of corresponding feeding events (right) recorded for each species: (*a*, *b*) *Pastinachus ater*, (*c*, *d*) *Pateobatis fai*, and (*e*, *f*) *U. granulatus*. Lines were coloured by species and feeding events by tidal-height category.

Effect of tide on ray foraging activity

Foraging rates, represented as the number of feeding events per hour, showed no significant differences on the basis of tracking length ($P = 0.70$) or year ($P = 0.89$). These variables were also insignificant predictors of proportion of time foraging per track (track length, $P = 0.11$; and year, $P = 0.76$). Thus, all tracks were interpreted collectively across both years and without further standardisation by track length.

Across the 96 tracks that were analysed, foraging rates and the proportion of time foraging per track both showed high variability across species and tidal-height categories (Fig. 5). The inclusion of tidal height and species in the foraging rate model explained 21.6% of the variance, with foraging rates exhibiting a negative relationship with tidal height ($\chi^2 = 22.92$, d.f. = 2, $P < 0.01$), but not with species ($\chi^2 = 5.60$, d.f. = 2, $P = 0.06$). Rays foraged most often during low tidal heights (mean = 37.5 ± 3.4 feeding events h^{-1}), followed by mid-tidal heights (mean = 34.4 ± 3.2 feeding events h^{-1}) and high tidal heights (mean = 9.1 ± 5.3 feeding events h^{-1}). Pairwise contrasts showed no difference in foraging rates between low and mid-tidal heights ($P = 0.77$). However, foraging rates decreased between low and high ($P < 0.01$) and between mid- to high tidal heights ($P < 0.01$) (Table 2).

Proportion of time foraging per track differed by tidal height ($\chi^2 = 29.19$, d.f. = 2, $P < 0.01$) and by species ($\chi^2 = 22.45$, d.f. = 2, $P < 0.01$), with tidal height and species collectively explaining 33.1% of the model variance. Rays collectively spent more time foraging at low tidal heights (mean proportion = 0.44 ± 0.04 of tracking time) than at mid- (0.28 ± 0.04) and high (0.11 ± 0.03) tidal heights. Proportion of time foraging per track decreased significantly between low and mid-tidal heights ($P = 0.04$), low and high tidal heights ($P < 0.01$), and mid- and high ($P = 0.00$) tidal heights (Table 2). By species, *P. ater* spent the most time foraging per track (mean proportion = 0.40 ± 0.04) compared with *P. fai* (0.19 ± 0.05) and *U. granulatus* (0.19 ± 0.03). Specifically, *P. ater* spent significantly more time foraging than did *P. fai* ($P = 0.00$) and *U. granulatus* ($P = 0.00$), whereas no differences were observed between *P. fai* and *U. granulatus* ($P = 1.00$) (Table 2).

Foraging preferences among ray species

Chi-Square analysis indicated an association between specific foraging types and substrate use ($\chi^2 = 71.47$, $P < 0.01$; Table S2). Specifically, rays used excavation more frequently on smooth sand (73.4% of feeding events) and the least on coral rubble (10.1%). Rays used suction feeding more frequently on coral rubble (42.1%) than on rubbly sand (21.1%) and smooth sand (36.8%). Surface feeding was most often used on smooth sand (73.9%), followed by rubbly sand (11.7%) and coral rubble (14.4%).

The model comparing substrate and foraging type preferences among species explained 78.8% of the total deviance. By substrate, *P. ater* was more likely to select smooth sand (mean = 54.2 ± 7.5% of feeding events) than coral rubble (7.9 ± 7.5%; $P < 0.01$), whereas no differences were observed between these substrates and rubbly sand (Fig. 6*a*, Table 3). By contrast, *U. granulatus* showed the highest probability of selecting coral rubble (87.2 ± 9.1%) over smooth sand (25.2 ± 9.2%; $P < 0.01$), and no differences were observed between combinations with rubbly sand. For *P. fai*, probability of feeding was greatest for smooth sand (20.6 ± 8.5%) and the least for coral rubble (4.9 ± 4.4%); however, these differences were insignificant (Table 3). By foraging type, *P. ater* was more likely to use excavation (mean prob. = 51.8 ± 11.2%) and least likely to use suction (7.0 ± 7.3%) ($P < 0.01$), whereas surface feeding (34.7 ± 9.3%) was preferred over suction ($P = 0.03$) but was similarly preferred to excavation ($P = 0.37$) (Fig. 6*b*, Table 3). *U. granulatus* had the highest probability of using suction (65.8 ± 10.8%) and exhibited similar preferences for surface (42.5 ± 8.2%) and excavation (42.4 ± 10.5%), although no combinations differed significantly. For *P. fai*, probabilities

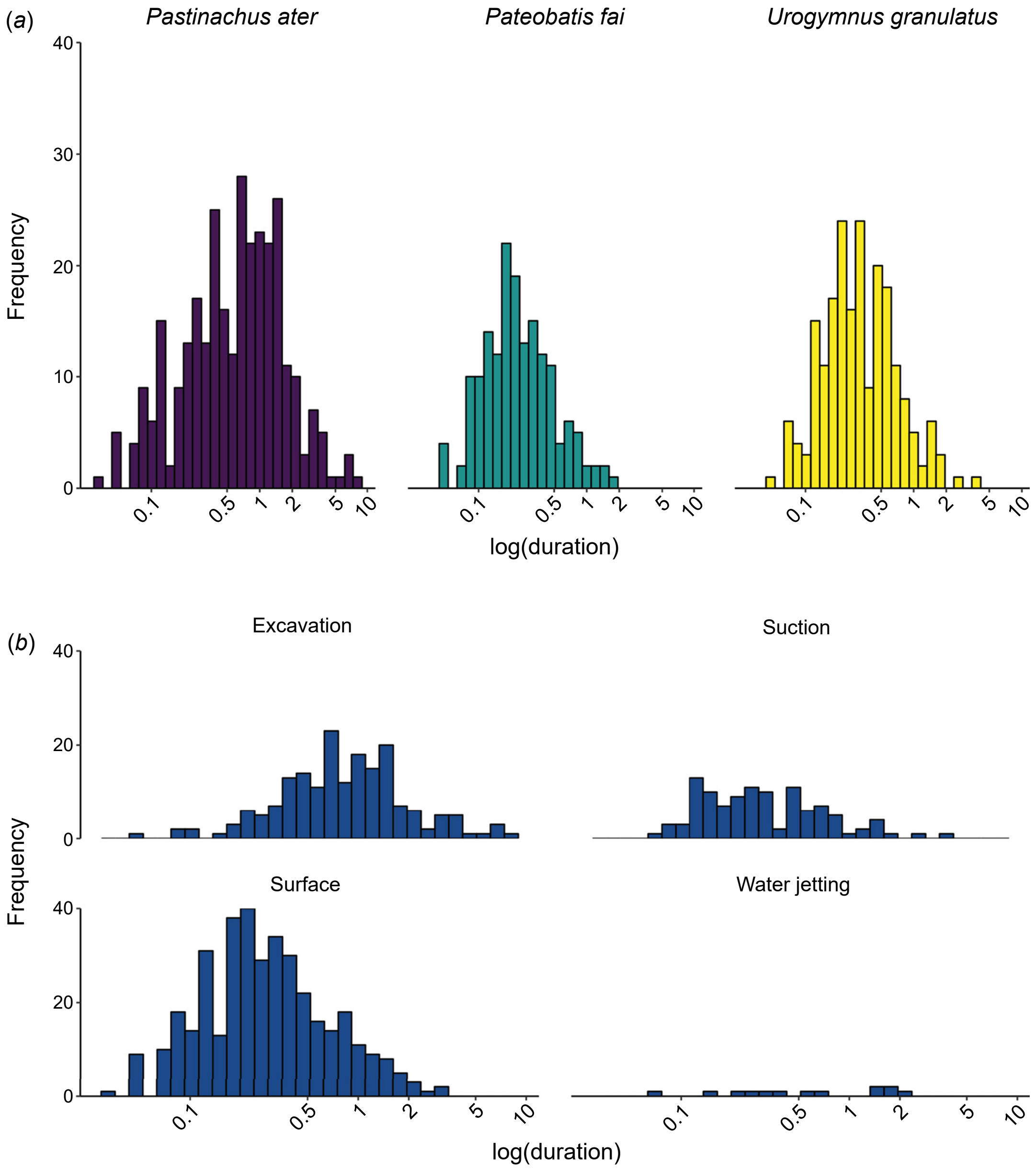

Fig. 4. Histograms showing the frequency distribution of feeding event duration (min) by (*a*) species and (*b*) foraging type. Log-transformation was applied to the *x*-axis for visualisation because of high skewness towards shorter feeding durations.

were similar for surface (22.8 ± 8.7%) and suction (27.2 ± 10.8%), and individuals were least likely to use excavation (6.1 ± 5.3%). However, these differences were insignificant (Table 3).

Pit or scar formation probability differed among species ($\chi^2 = 39.41$, d.f. = 2, $P < 0.01$), with the model explaining 35.4% of the total variance (Fig. 7). Pit or scar formation was greatest for *P. ater* (53.2 ± 4.8%), being approximately seven-fold greater than that for *P. fai* (7.6 ± 2.7%; $P < 0.01$) and two-fold greater than that for *U. granulatus* (27.0 ± 5.6; $P < 0.01$). Pit or scar formation for *P. fai* was 19.4% less than that for *U. granulatus* ($P < 0.01$) (Fig. 7, Table 3).

Discussion

Temporal foraging patterns over the tide

The periodic movements of rays across the intertidal gradient (Ruiz-García *et al.* 2020; Oleksyn *et al.* 2021*b*; Elston *et al.* 2022) inherently determine where foraging can occur at a given time. In these dynamic environments, foraging patterns were expected to follow one of the following two different strategies: (1) rays would feed continuously as they exploit available habitats across the tidal cycle (Wetherbee *et al.* 2004),

Table 1. Metrics of feeding event duration by species and foraging type.

Item	Number of feeding events	Minimum duration (min)	Median duration (min)	Maximum duration (min)
Species				
P. fai	168	0.05	0.22	1.67
U. granulatus	212	0.05	0.32	3.80
Foraging type				
Excavation	184	0.05	0.81	8.33
Suction	108	0.07	0.26	3.80
Surface	376	0.03	0.27	3.43
Water jetting	13	0.07	0.57	2.28

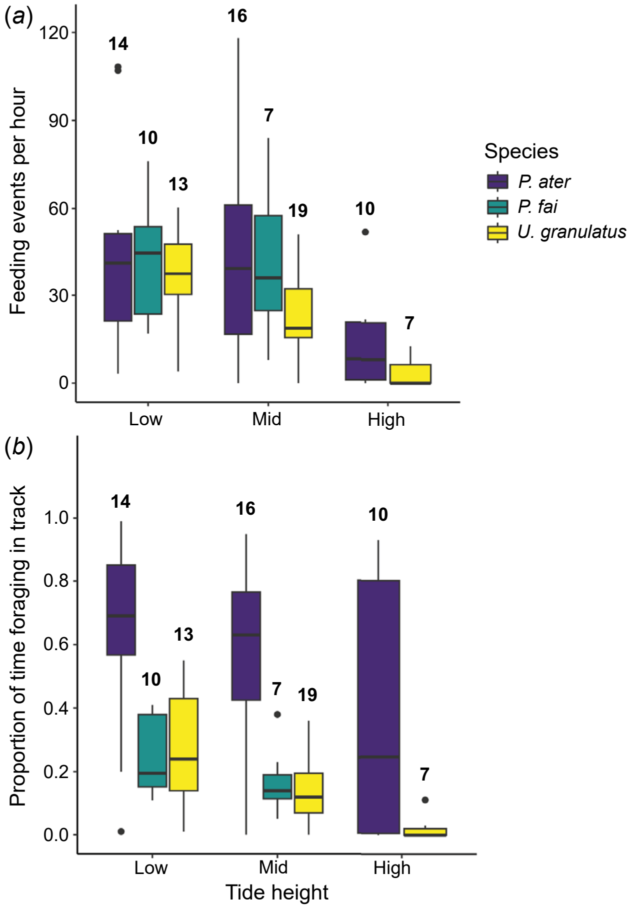

Fig. 5. Boxplots showing (*a*) the number of feeding events per hour and (*b*) the proportion of time foraging per track (seconds of foraging divided by total tracking time) across three tidal-height categories (low = 0.1–1.5 m, mid = 1.6–2.2 m, high = >2.2 m). Numbers above the bars denote the number of tracks (tracked rays) for each category. Outliers were retained in the plots for visualisation.

Table 2. Pairwise contrasts between the predicted marginal means of each foraging metric by tidal-height category (low = 0.1–1.5 m, mid = 1.6–2.2 m, high = >2.2 m) and ray species.

Contrast	Difference	*t*-ratio	*P*-value
Foraging rate			
Tidal-height category			
Low *v.* high	28.4	4.57	**<0.01**
Low *v.* mid	3.1	0.68	0.77
Mid *v.* high	25.3	4.26	**<0.01**
Species			
P. ater v. P. fai	−4.4	−0.72	0.75
P. ater v. U. granulatus	8.1	1.77	0.18
P. fai v. U. granulatus	12.5	2.10	0.09
Prop. time foraging per track			
Tidal-height category			
Low *v.* high	0.30	6.25	**<0.01**
Low *v.* mid	0.20	2.56	**0.04**
Mid *v.* high	0.17	3.88	**<0.01**
Species			
P. ater v. P. fai	0.21	3.44	**<0.01**
P. ater v. U. granulatus	0.21	4.52	**<0.01**
P. fai v. U. granulatus	0.00	0.08	1.00

Differences in foraging rate are given in number of feeding events per hour, and proportion of time foraging per track as the differences in mean proportions. Positive differences indicate a higher mean value for the first group (s.e. = ±1 standard error). Statistically significant differences ($P < 0.05$) are denoted in bold text.

or (2) rays would concentrate foraging efforts during periods when preferred foraging patches become available (MacArthur and Pianka 1966; Burrows 1994). At lower tidal heights in Pioneer Bay, rays fed along the subtidal edges near the reef crest. Foraging then extended to newly submerged habitats closer to the beach and mangrove edges as these became accessible with rising tides. In this case, foraging appeared to be opportunistic, with rays feeding across different microhabitats as they moved into upper intertidal habitats.

Pastinachus ater foraged more frequently within the Pioneer Bay reef flat during lower tidal heights, showing an inverse relationship with water depth. This pattern matches previous observations at this location, where members of this species commonly rest along the mangrove edges or on open sand flat patches during high tides (Martins *et al.* 2020). Temporal foraging patterns were most evident for *U. granulatus*. As with *P. ater*, this species fed most actively during lower tidal-height levels over both smooth sand and rubbly substrates dispersed across the middle and outer flat areas. In five of the seven tracks collected for *U. granulatus* during high tidal heights, the tracked ray spent most of the tracked time resting or buried near the mangrove edges, with little or no feeding observed. This pattern is likely to reflect its preferences for occupying mangrove stands during rising and high tides, where it generally remains as long as water levels permit (Davy *et al.* 2015; Martins *et al.* 2021).

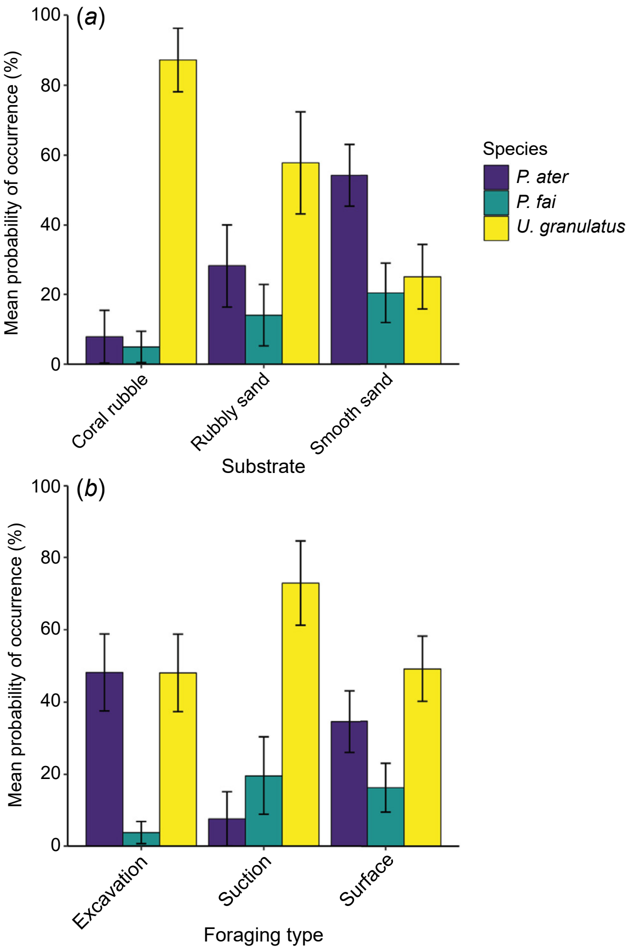

Fig. 6. Predicted probability percentages (±1 s.e.) of feeding events by (*a*) substrate and (*b*) foraging type for each ray species.

Aerial surveys could not reliably assess feeding activity in the mangroves, because the root structures obstructed visibility from overhead. However, ground-level observations of *U. granulatus* in the mangroves showed that individuals commonly rested alone or in small groups (J. Myers, pers. obs.). Although some foraging within mangrove habitats has been documented using stationary video (Kanno *et al.* 2019), the importance of mangroves as feeding grounds relative to other available habitats is uncertain. We note that differences in foraging rates owing to tidal height were not observed for *P. fai*, although this may have been due to an absence of data during high tidal ranges and lower sample sizes for this species.

External factors linked to tidal habitat accessibility may also influence how rays forage within the reef flat. Benthic invertebrate communities in intertidal flats vary significantly across tidal submergence gradients in tropical tidal flats (Dittmann 1995, 2000), with some studies showing greater benthic invertebrate densities in the lower intertidal zone (Dittmann 2000; Sheaves *et al.* 2016). The accessibility of these prey types during lower tidal levels may explain the prevalent ray foraging activity on the outer flat while these

Table 3. Pairwise contrasts between the predicted marginal means (probabilities) of a ray species selecting each substrate or foraging type.

Species	Contrast	Difference (%)	s.e.	*z*-ratio	*P*-value
	Substrate				
P. ater	Coral rubble *v.* rubbly sand	−20.3	12.7	−1.60	0.25
	Coral rubble *v.* smooth sand	−46.4	11.3	−4.10	**<0.01**
	Rubbly sand *v.* smooth sand	−26.0	13.8	−1.88	0.14
P. fai	Coral rubble *v.* rubbly sand	−9.1	9.2	−0.98	0.59
	Coral rubble *v.* smooth sand	−15.6	9.3	−1.69	0.21
	Rubbly sand *v.* smooth sand	−6.6	10.5	−0.63	0.81
U. granulatus	Coral rubble *v.* rubbly sand	29.4	15.4	1.91	0.14
	Coral rubble *v.* smooth sand	62.0	12.6	4.94	**<0.01**
	Rubbly sand *v.* smooth sand	32.6	15.8	2.05	0.10
	Foraging type				
P. ater	Excavation *v.* suction	40.7	12.7	3.21	**<0.01**
	Excavation *v.* surface	13.6	10.1	1.35	0.37
	Suction *v.* surface	−27.1	10.8	−2.51	**0.03**
P. fai	Excavation *v.* suction	−15.8	10.9	−1.45	0.31
	Excavation *v.* surface	−12.5	6.4	−1.93	0.13
	Suction *v.* surface	3.4	11.2	0.30	0.95
U. granulatus	Excavation *v.* suction	−24.8	15.0	−1.66	0.22
	Excavation *v.* surface	−1.2	10.5	−0.11	0.99
	Suction *v.* surface	23.7	13.3	1.79	0.18
	Pit or scar formation				
	P. ater v. P. fai	45.6	5.6	8.19	**<0.01**
	P. ater v. U. granulatus	26.2	7.5	3.51	**<0.01**
	P. fai v. U. granulatus	−19.4	6.2	−3.15	**<0.01**

Species were compared directly for pit or scar formation. For ease of interpretation, differences in mean values and s.e. (±1 s.e.) are given as percentages. Positive differences indicate a higher mean for the first group. Statistically significant ($P < 0.05$) differences are denoted in bold.

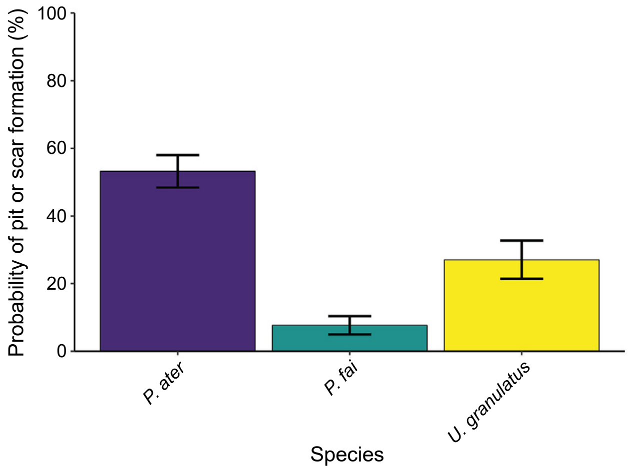

Fig. 7. Predicted probability percentages (±1 s.e.) of each species creating a feeding pit or scar on either smooth sand or rubbly sand substrates.

areas are shallowly inundated, and new prey types become available during the low–high progression. Rays must also make trade offs between prey availability and predator avoidance as water depth increases (Vaudo and Heithaus 2013; Davy *et al.* 2015; Sherman *et al.* 2020). Several shark species that are known to target rays including sharptooth lemon sharks, (*Negaprion acutidens*) and great hammerhead sharks (*Sphyrna mokarran*) are common on the reef flat (Schlaff *et al.* 2017; Martins *et al.* 2022; Lubitz *et al.* 2023), and predation attempts on rays have been observed directly at Pioneer Bay (A. Martins, pers. obs; J. Myers, pers. obs.) and at nearby Lucinda Beach (Lubitz *et al.* 2023). Thus, rays may invest more time in predator avoidance behaviours such as burying or using structural refuges during times when larger predators have greater access to the upper intertidal zone (Semeniuk and Dill 2005, 2006; Bond *et al.* 2019).

Foraging preferences among ray species

Species-specific foraging behaviours provided evidence of fine-scale resource partitioning within the reef flat. However, high overlap in specific aspects of foraging, such as all three species using surface feeding on smooth sand (albeit in different proportions) and feeding over similar habitat areas suggested that all three species share some degree of functional redundancy. Whereas resource partitioning enables species coexistence by minimising interspecific competition (Schoener 1974; Walter 1991; Saulnier *et al.* 2020), differences in foraging patterns across microhabitats and sediment depths may be shaped by species-specific morphological and behavioural adaptations rather than as a direct response to competition (Motta and Huber 2004; Wetherbee *et al.* 2004).

Associations between substrate choice and foraging type demonstrated that rays selected specific foraging behaviours depending on the substrate, or conversely, that some substrates are more compatible with the preferred foraging types of each species. Both *P. ater* and *P. fai* predominantly used surface feeding on smooth sand, suggesting that these species may target similar prey resources from the surface layers of substrate. However, *P. ater* also used excavation feeding more than did all other species, which was associated with greater sediment disturbance and may enable this species to access deeply buried prey. A previous study by Crook *et al.* (2022) similarly documented high levels of surface feeding by *P. ater*, albeit with fewer occurrences of excavation. Results from both studies suggest that these two foraging behaviours are conserved by this species. The predominance of certain foraging types may reflect differences in microhabitats (e.g. substrate composition) and prey availability between the unvegetated sand flats at Lucinda Beach *v.* the rubble-strewn reef flats at Orpheus Island. Overall, more data would be needed to characterise foraging strategies across a broader range of ecological contexts.

Foraging of *U. granulatus* was the most distinct from other species because of greater preferences for feeding among coral rubble. In rarer cases, individuals even manipulated or fully rotated coral rubble fragments with their rostra (a behaviour that was unique to this species). Two feeding events also occurred along the rocky edge bordering the northern end of the bay, further demonstrating their ability to feed on the reef structure. Because coral rubble was most associated with both suction and surface feeding, rays may use surface feeding if a target prey is located along the surface of the coral, whereas suctioning water into the buccal cavity would be more effective for drawing out concealed prey from the crevices (Wilga and Motta 1998; Shibuya *et al.* 2012). Although mouth morphology and dentition are also expected to influence species-specific foraging capabilities and subsequent dietary composition (Pardo *et al.* 2015; Kolmann *et al.* 2023), a lack of morphological data for these species precludes further inspection into these relationships.

Previous studies comparing dietary and trophic niches between *U. granulatus* and *P. ater* have reported little overlap between the species, with the former specialising on decapod crustaceans and the latter consuming a broader mix of bivalves, crustaceans and annelids (Crook 2020; Elston *et al.* 2020; Martins *et al.* 2022). Combining knowledge of species diets and foraging behaviours provides some indication as to which prey types may be associated with specific behaviours. For example, higher frequencies of excavation feeding (used almost exclusively by *P. ater*) may be more associated with extracting polychaetes or other infaunal prey, which may be less important in the diets of other species (Myers *et al.* 2025). Additionally, the distinct dietary niches of *U. granulatus* could reflect preferences for decapod crustaceans that are associated with structural habitats (e.g. coral). However, proper analyses of each species' diets would be needed to verify whether this is the case. Given that trophic niches have been investigated only for *P. ater* and *U. granulatus* in Pioneer Bay, it remains unclear how much dietary overlap they share with *P. fai*. On the basis of observations alone, the shared preferences of bare sand and surface feeding by both *P. fai* and *P. ater* suggest that they may share more dietary overlap with each other than with *U. granulatus*. However, previous studies on *P. fai* and related whipray species (genus *Himantura*) from other nearshore habitats in Australia have shown their diets to vary significantly from those of *P. ater*, with greater consumption of decapod crustaceans (Vaudo and Heithaus 2011; O'Shea *et al.* 2013; Myers *et al.* 2025).

The presence of multiple species performing complementary functional roles is a critical driver of ecosystem function (Hooper *et al.* 2012). Comparing foraging behaviours among three ray species illustrated the diversity of functional roles that ray communities perform over localised scales, as well as their potential contributions to ecosystem-level bioturbation. Whereas all ray species modified the environment through feeding pits or scars, *P. ater* was more likely to create feeding pits (>50% of all feeding events) than was *U. granulatus* (27%) or *P. fai* (8%). Species differed in their use of disruptive (excavation, suction, water jetting) *v.* non-disruptive (surface) foraging types. Across all four behaviours, excavation appeared to be associated with greater levels of sediment disturbance and feeding pit formation. This was supported by quantifications of bioturbation at the Lucinda sand flat, where excavation accounted for 58–67% of sediment turnover and the largest pits, despite occurring in fewer feeding events (Crook *et al.* 2022). Because this foraging type was preferred more exclusively by *P. ater*, it is likely to contribute more substantially to bioturbation of soft sediments than do sympatric species.

Foraging across different substrates demonstrates the ability of rays to influence macroinvertebrate communities through different trophic pathways. For instance, unvegetated sand flats typically support burrowing infauna such as polychaetes, bivalves and small crustaceans (Pacheco *et al.* 2011), whereas reef substrates harbour more epibenthic taxa including decapod crustaceans, amphipods and molluscs that are adapted to structural complexity (Stella *et al.* 2010; Plaisance *et al.* 2011). Additionally, the vertical distribution of invertebrates throughout the sediment column determines which prey types are accessible to different ray species, because of their unique morphologies and foraging capabilities (Kolmann *et al.* 2015; Wilga and Ferry 2015). Therefore, by disproportionately selecting coral rubble, *U. granulatus* may play a more pivotal role in regulating populations of coral-associated prey taxa, whereas *P. ater* and *P. fai* would apply more predation pressures on invertebrate taxa that are associated with soft-bottom habitats.

Conclusions

The pervasiveness of foraging activity by juvenile *P. ater*, *P. fai* and *U. granulatus* demonstrated that these species regularly obtain resources within the Pioneer Bay nursery. Moreover, species use diverse tactics to feed in response to tidal habitat availability and exploit different microhabitat niches within the intertidal zone. These findings also provided the first detailed descriptions of foraging behaviours for *P. fai* at this location, as well as insights into their potential trophic niches and interactions with sympatric species. Importantly, despite superficial morphological and ecological similarities among these dasyatid stingray species, the observed differences in foraging behaviours suggest how they exert distinct biophysical pressures on intertidal ecosystems by ecosystem engineering (e.g. pit formation) and trophic interactions.

Some limitations were apparent from this study, such that behaviours of individual rays were analysed over short periods (maximum of 18 min). Thus, although drone tracking provided a high-resolution ‘snapshot’ of foraging, these data may potentially exclude rare feeding events, or yield little information if feeding frequency is low or if visibility is obscured by unfavourable weather conditions. Where greater temporal coverage is required, future studies could consider extending the tracking duration using overlapping drone deployments (Crook *et al.* 2022) or by combining drones with complementary observational techniques (e.g. stationary cameras). Moreover, with data collection restricted to two site visits, certain factors could not be investigated, such as the effect of time of day on foraging. Moreover, further research is needed to understand the full extent of temporal variability, such as trade offs between foraging and thermal tolerance (Higgins *et al.* 2024) or if predator avoidance behaviours differ between spring and neap tides. Collectively, such efforts would advance our understanding of the complex interplay between resource acquisition, predator avoidance and physiological constraints on ray behavioural ecology.

Continued exploration of ray foraging behaviours will provide critical insights into the strategies that develop within multi-species communities to potentially minimise competition, and how fine-scale patterns contribute to functional diversity at ecosystem scales (Duffy 2002; Hooper *et al.* 2005; Leduc *et al.* 2015). Aside from this study, virtually no efforts have been undertaken to compare foraging behaviours among ray species (however, see Crook *et al.* 2022). Thus, it is clear that more research is needed to understand whether species-specific behaviours reliably translate to differences in their trophic ecology, and whether preferences for specific foraging types are conserved across other ecological contexts. Integrating such information with benthic prey surveys across various microhabitats and sediment depths will provide more definitive linkages between behaviours observed here and prey selection. Moreover, because the specific contributions of rays to processes such as bioturbation and nutrient dynamics can be difficult to quantify in the field (Flowers *et al.* 2021), future *in situ* experiments could be particularly useful for bridging the gaps between specific behaviours and functional outputs, and for understanding the scales over which these processes occur.

Supplementary material

Supplementary material can be accessed from the article page online.

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Data availability. Data are archived in the Research Data JCU repository at James Cook University, Australia. The data publication has been reviewed and published on the JCU data portal (see Myers and Crook 2026).

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