

Visual-chemotactic saltatory search in *Octopus hummelincki* (Mollusca, Cephalopoda): a case study in the South Atlantic

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ABSTRACT

We report for the first time evidence of foraging by *Octopus hummelincki* and analyze it using saltatory search theory, which posits alternating phases of locomotion and stationary search. Our data showed that substrate complexity dictates behavioral transitions: locomotion predominated in sand, whereas solid substrates elicited tactile exploration. The move-to-search scaling ratio (0.63) aligns with the 2/3 power-law prediction for optimal intermittent searchers. Poke duration was shorter when preceding successful captures than during unsuccessful ones. These findings suggest that *O. hummelincki* employs optimized, multisensory-integrated search strategies, in which the move-pause balance reflects high-level cognitive processing. The integration of visual and chemotactile information minimizes energy expenditure and maximizes predatory success in benthic environments.

KEYWORDS: Cephalopods, ethogram, foraging, giving-up time, sensory system.

INTRODUCTION

Foraging in complex environments requires balancing movement and active prey seeking, a trade-off that drives the evolution of optimized search strategies. Saltatory Search Theory posits that some animals employ a stop-and-go strategy, alternating between displacements and pauses to detect prey (O'Brien et al. 1990). During these pauses, the animal reduces self-generated noise, increasing the probability of encountering targets (Forbes et al., 2025). The “search phase,” during which the animal remains stationary to scan the environment, is followed by a “move phase” that emphasizes movement (Bénichou et al. 2005). While this model has been validated in the visual modality (Rischawy & Schuster 2013), its application to non-visual sensory systems remains unexplored.

Octopuses are ideal models for testing saltatory strategies due to their multimodal sensory systems and cognitive complexity (Hanlon & Messenger 2018). While stop-and-go patterns have previously been studied through a visual lens (Mather 1991; Leite et al. 2009; Bennice et al. 2021), benthic foraging is a visual-chemotactile task (Yarnall 1969) in which traditional pauses are replaced by active ‘Poking’ and tactile-chemical exploration (Mather 1991). Upon detection, octopuses execute a ‘Web over’ or ‘Parachute attack’ (Yarnall 1969), spreading the interbranchial membrane to trap and capture prey. *In situ* experiments demonstrate that octopuses perform the maneuver significantly more frequently in locations with confirmed prey presence than in empty burrows, consolidating the web as the tactical outcome that guarantees successful capture (Sampaio et al. 2024).

Here, we report for the first time evidence of the foraging strategy of a juvenile *Octopus hummelincki* Adam in its natural habitat and determine whether its behavioral patterns follow saltatory search theory. By analyzing behavioral transitions and testing our data against the “optimal search” ratios (Bénichou et al. 2005), we aim to demonstrate how cognitively optimized search models validated in the visual modality can extend to the visual-chemotactile foraging of marine animals.

MATERIAL AND METHODS

Species analyzed, field characterization, and data collection

One individual of *Octopus hummelincki* (Fig. 1) was filmed using the Focal Animal Sampling method (Altmann 1974) in December, 2024 via snorkeling at Búzios Beach, Brazil. The species

was identified based on the presence of ocelli, the morphological pattern of its papillae, a small body size, and the chromatic skin patterns (cf. Burgess 1966).

The videos were analyzed using *Solomon Coder* software. A second trained coder independently analyzed a subsample of videos (n=6). The data, originally collected frame-by-frame (0.2s), were converted to total event durations. Reliability was measured using the intraclass correlation coefficient. The agreement index obtained was greater than 0.98 for all behavioral categories.

Given the species' elusive nature, we treated multiple video sessions as independent observation units to assess behavioral consistency.

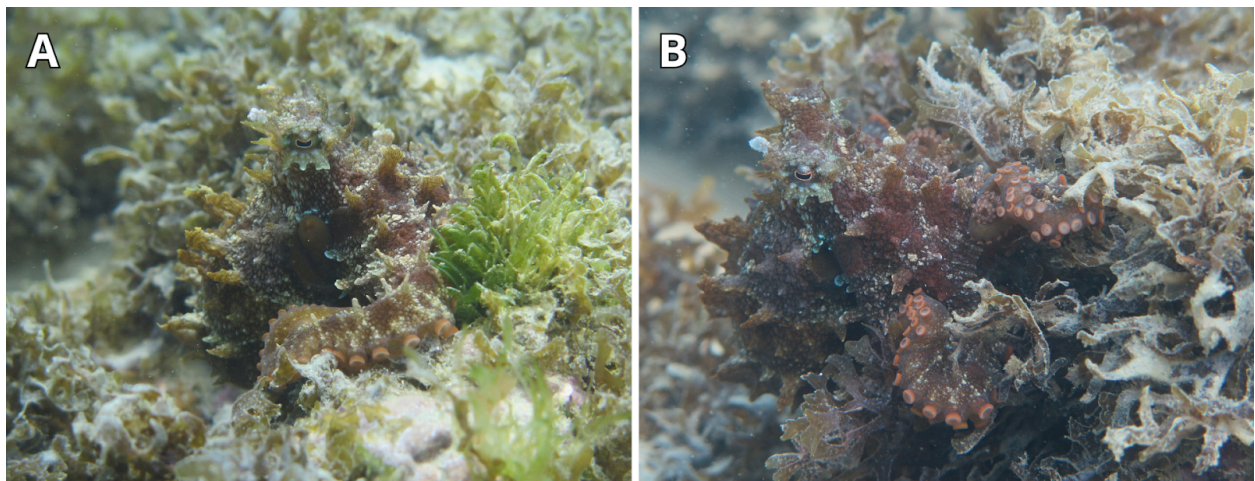


Fig. 1. *Octopus hummelincki*. (A) Stationary and (B) Crawling on the substrate. (Photos: MPA).

Behavioral categories

The behaviors were classified according to Mather and Alupay (2016). We identified four behaviors: (1) ‘Crawl’, as arm-mediated locomotion; (2) ‘Poke’, as an active pause in which the animal inserts one or more arms into substrate; (3) ‘Pounce’, a rapid (< 1 second) target-guided lunge; and (4) ‘Web over’ or ‘Parachute attack’ (cf. Yarnall 1969), the spread arms and expansion of the interbrachial membrane over the substrate to engulf potential prey.

Statistical Analysis

Statistical significance was set at $P=0.05$ (mean \pm SD). Since Shapiro-Wilk tests indicated non-parametric distributions, we used non-parametric methods for all comparisons. Substrate effects on decision-making were analyzed using the Kruskal-Wallis test across rock, algae, and

sand substrates. Total time budgets were calculated to verify the consistency of patterns across substrates.

Mann-Whitney U tests compared time investments between locomotion and investigation, and between poke and crawl, while variance was used to assess motor plasticity. Foraging optimization was tested against intermittent search models (Bénichou et al. 2005) by calculating the move-to-search scaling ratio (T2: crawl / T1: poke), with values between 0.60 and 0.66 indicating efficiency.

To evaluate how search outcomes influenced behavior, Mann-Whitney U tests were used to compare durations between outcomes (capture vs. non-capture). A linear mixed-effects model was applied to assess how ‘Web over’ impacted ‘Poke’ duration. The data were log-transformed to ensure normality and homoscedasticity, with ‘Webover’ set as a fixed effect and “Video_ID” as a random effect to control for dependence across sessions.

RESULTS

Substrate-specific behavioral plasticity

The observed *O. hummelincki* modulates its behavior in response to substrate type ($P < 0.05$; see Supplementary Material). ‘Crawl’ was predominant in sandy areas, occupying an average time proportion of 0.83, higher than in other habitats ($P < 0.001$). ‘Poke’ was the primary strategy on structured substrates, with averages of 0.64 on algae and 0.52 on rock ($P < 0.001$). ‘Web over’ occurrence tended to be higher in rocky substrates (0.20), though not significantly so ($p = 0.076$); while ‘Pounce’ showed no statistical variation among habitats ($P = 0.635$).

Movement-pause dynamics and intermittent search optimization

The foraging activity comprised 331 behavioral events. The behavioral repertoire was dominated by ‘Crawl’ and ‘Poke’ (89.4% of occurrences). Although ‘Crawl’ and ‘Poke’ showed similar frequencies ($n = 152$, 45.9% and $n = 144$, 43.5%, respectively), their temporal investment revealed distinct strategic priorities. While ‘Crawl’ served as a frequent but brief locomotor transition, ‘Poke’ consumed the largest share of the total foraging budget (51.60%; 11.8 min). In contrast, high-intensity capture behaviors were less frequent, with ‘Web over’ occurring 33 times (10.0%) and ‘Pounce’ occurring only two times (0.6%).

Stationary search events (‘Poke’ and ‘Web over’: 5.40 ± 4.59 s, $n = 185$) were significantly

longer than locomotor events ('Crawl' and 'Pounce': 3.54 ± 1.97 s, $n=146$) ($P < 0.001$; Fig. 2A). 'Poke' events were longer than 'Crawl' ones ($P=0.001$) (Fig. 2B), and exhibited both higher mean duration and greater variability (5.60 ± 4.89 s) compared to 'Crawl' (3.56 ± 1.97 s).

The mean duration 'Crawl' was 3.56 ± 1.97 s, while 'Poke' lasted an average of 5.60 ± 4.89 s. The resulting scaling ratio between these two states was 0.635. The overall time budget allocation reflected a similar pattern of optimization: *O. hummelincki* spent 38% of its active foraging time in the move phase and 62% in the search phase, yielding an intermittency ratio of 0.613, which closely approximates the 3/5 (0.60) power law.

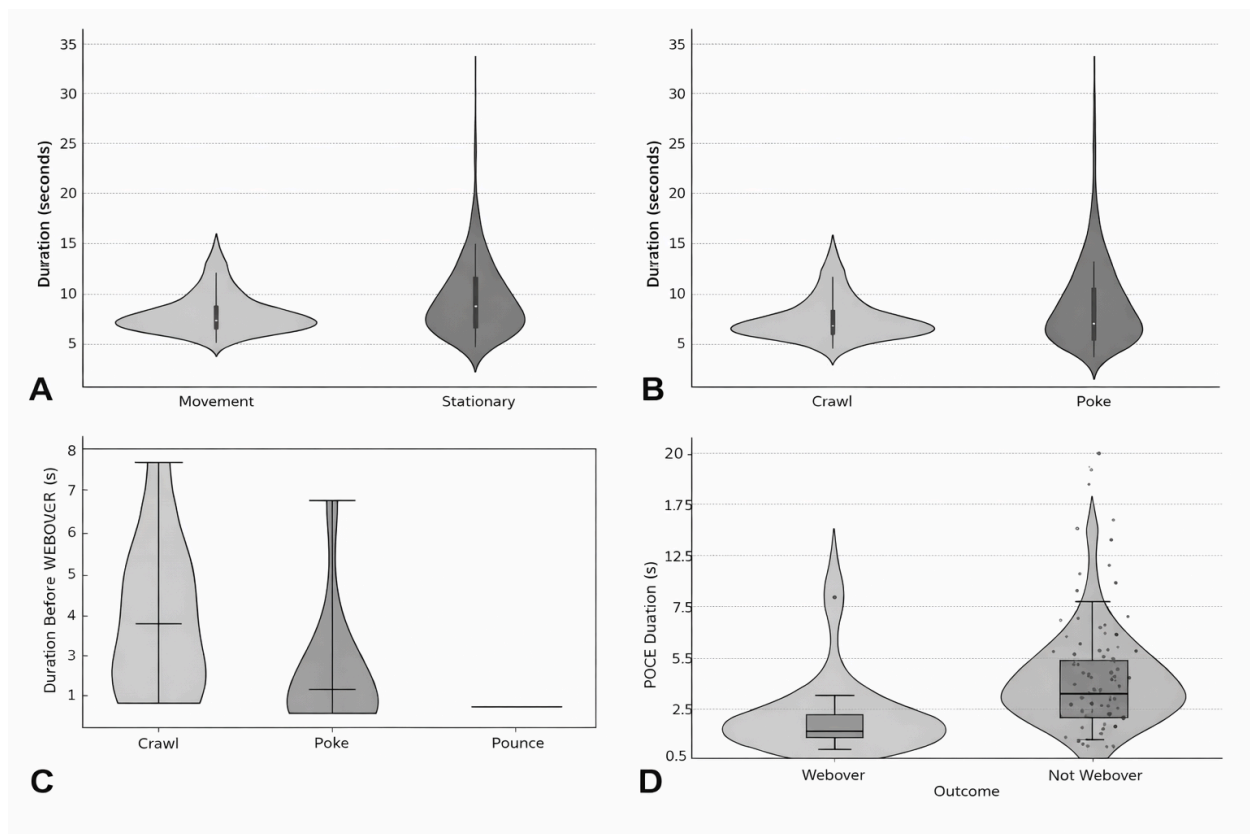


Fig. 2. Durations and outcomes of foraging behaviors in *O. hummelincki*. (A) Comparison of event durations between broad foraging states; (B) Duration of individual events for locomotor (Crawl, $n=144$) and localized tactile investigation (Poke, $n=152$) behaviors; (C) Duration of behaviors (crawl, poke, and pounce) immediately preceding a webover event; (D) Distribution of poke duration as a function of the search outcome ('Web over' vs. 'Non Web over').

Chemotactile search duration

The duration of behaviors immediately preceding ‘Web over’ differed ($P=0.01$; see Supplementary Material) (Fig. 2C). ‘Crawl’ showed the longest average durations (3.69s), followed by ‘Poke’ (1.65s) and ‘Pounce’ (0.8s) ($P=0.0101$).

When ‘Poke’ was successful, followed by ‘Web over’, the mean ‘Poke’ time was 2.36 ± 3.00 s (Median= 1.30s; $n=16$). In contrast, the unsuccessful search mean time was longer, reaching 4.89 ± 3.78 s (Median = 3.80s; $n=129$). The Mixed Model confirmed that the occurrence of ‘Web over’ has a significant and negative predictive effect on ‘Poke’ duration ($P<0.001$). The variance associated with the random effect of the videos was minimal, indicating that the reduction in ‘Poke’ time before the encounter is a consistent behavioral pattern (Fig. 2D).

DISCUSSION

Although this study is based on a single *Octopus hummelincki*, the high temporal resolution achieved through frame-by-frame analysis across 31 independent foraging sessions yields a sound dataset. Such in-depth observations allowed testing the theoretical boundaries of available foraging models.

The foraging behavior observed here provides empirical support for the saltatory search theory, indicating that the stop-and-go pattern is a cognitively optimized strategy. Behavioral modulation reflects a sophisticated resource-exploitation strategy in which substrate complexity shapes transitions between phases. While locomotion prevails in open areas, complex substrates elicit intensive tactile investigation. These stop-and-go sequences align with saltatory tactics in other octopus species (Bennice et al. 2021), suggesting that stationary windows are fine-tuned investments to maximize prey detection in heterogeneous environments.

The observed ratio between the average durations of ‘Crawl’ and ‘Poke’ yielded a scaling factor of 0.635, which closely matches the theoretical optimal of 0.66 for efficient searchers; the total time budget (38% movement and 62% stationary search) yielded a ratio of 0.613, nearly identical to the 0.60 efficiency peak described by Bénichou et al. (2005). Optimal intermittent search models may be described as a "time-minimizing hunter" that reduces exposure to predators while maximizing net energy gain, as observed in *O. insularis* (Leite et al. 2009).

This efficient search strategy relies on a multisensory cognitive approach rather than vision alone. Similar to how lateral-line predators pause to reduce self-generated sensory input and better detect prey (Bassett et al. 2007), the octopus's ‘Poke-Crawl’ alternation suppresses

movement-related sensory noise, filtering chemical and tactile substrate cues. This behavior indicates a cognitive “switch” between modalities: displacement is guided visually, while localized searching is primarily chemotactic. This prolonged sensory sampling mirrors mammalian behavior (Banerjee & Bhadra 2022), suggesting that the 2/3 scaling law of intermittent search (Bénichou et al., 2005) can represent a shared evolutionary adaptation across taxa for managing information-heavy sensory systems.

The significantly shorter duration of ‘Poke’ preceding a ‘Web over’ compared to a ‘non Web over’ corroborates Anderson’s (1981) predictions on giving-up time. Immediate prey detection works as a biological stop signal, whereas longer durations in empty crevices reflect the predator’s investment in confirming the absence of resources. Regarding the capture itself, in *O. cyanea* the ‘Web over’ time varied from 0.75 to 2.16 seconds (Yarnall 1969), while the average duration in *O. hummelincki* was 4.45 seconds. This is notably shorter than the 40–60 seconds reported for *O. cyanea* by Sampaio et al. (2024).

The integration of the variability in giving-up time in *O. hummelincki* with Vermeij’s (1982) theory suggests that unsuccessful predation shapes sensory specialization. While Vermeij argues that prey survival enables the evolution of defenses, prolonged poking into empty crevices reveals the cost of overcoming crawling and camouflage. Thus, predator persistence and prey resistance co-evolve: the octopus invests time to minimize detection failures against prey that have evolved to remain below its recognition threshold.

Our results suggest that longer, more variable durations of the stationary phases reflect selective attentional investment. The detection of cryptic targets requires heightened neuronal activity (Moran & Desimone, 1985), which helps explain why the octopus prioritizes local investigation over movement speed. While attentional bottlenecks in primates limit visual processing (Dukas 2004), a similar constraint likely governs chemotactile foraging in *O. hummelincki*. The prolonged duration and six-fold higher variance of ‘Poke’ events likely reflect the temporal cost of sensory integration, which is essential for resolving target ambiguity (Grasso & Basil 2009). These findings support the search rate hypothesis (Gendron & Staddon 1983), as *O. hummelincki* manages the trade-off between search rate and detection probability by investing time to overcome the challenges of detecting hidden targets.

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DISCLOSURE STATEMENT

The authors declare no conflict of interest.

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ETHICAL STANDARD

We comply with the standards set out in Directive 2010/63/EU and also the ethical standards proposed by the Wild Animal Initiative.

AUTHOR CONTRIBUTION

Conceptualization: MPA, FA, CMDS, JM; Methodology: MPA, FA, CMDS, JM; Software: MPA, FA; Investigation: MPA, FA, CMDS, JM; Data Curation: MPA, FA, CMDS, JM; Formal analysis: MPA, FA; Writing – original draft preparation: MPA, FA, CMDS, JM; Writing – review & editing: MPA, FA, CMDS, JM; Supervision: CMDS, JM; Funding acquisition: MPA, CMDS. All authors have read and agreed to the published version of the manuscript.

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DATA ACCESSIBILITY

Data available upon request to the authors.

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SUPPLEMENTARY MATERIAL

Table S1. Substrate-specific behavioral modulation and plasticity in *Octopus hummelincki*.

Behavior	Substrate	Mean time proportion	p-value
Crawl	Sand	0.83	p < 0.001
Poke	Algae	0.64	p < 0.001
Poke	Rock	0.52	p < 0.001
Web over	Rock	0.20	p = 0.076
Pounce	All	N/A	p = 0.635

Table S2. Move-pause dynamics and intermittent search optimization metrics (Total events = 331).

Metric / Behavior	Frequency (n)	Percentage (%)	Mean duration ± SD (s)	Statistical comparisons
Crawl	152	45.9%	3.56±1.97	Frequent but brief locomotor transition; <i>Poke</i> vs <i>Crawl</i> : p = 0.001
Poke	144	43.5%	5.60±4.89	Consumed the largest share of the foraging budget (51.60%); higher variability.
Web over	33	10.0%	4.45	High-intensity physical restraint and capture mechanism.
Pounce	2	0.6%	< 1.00 s	Rapid, target-guided lunge toward a specific target.
Stationary Events (<i>Poke</i> + <i>Web over</i>)	185	55.9%	5.40± 4.59	Significantly longer than locomotor events (p < 0.001).
Locomotor Events (<i>Crawl</i> + <i>Pounce</i>)	146	44.1%	3.54±1.97	Emphasizes the displacement and movement phase.

Table S3. Chemotactile search duration and giving-up time outcomes.

Analyzed Variable	Preceding condition/behavior	Value (Mean / Median)	p-value	Applied statistical model
Duration of behaviors immediately preceding <i>Web over</i>	Crawl	3.69 s	p = 0.01	Non-parametric methods (Kruskal-Wallis / Mann-Whitney U).
	Poke	1.65 s		
	Pounce	0.80 s		
Distribution of <i>Poke</i> duration by search outcome	Successful Search (<i>Web over</i>)	Mean: 2.36±3.00 s	p < 0.001	Linear Mixed Effects Model (LMM) with log-transformed data.
		Median: 1.30 s (n=16)		
	Unsuccessful Search (No <i>Web over</i>)	Mean: 4.89±3.78 s		
		Median: 3.80 s (n=129)		