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Navigating Nature's Terrain: Jumping Performance Robust to Substrate Moisture and Roughness by Blackspotted Rockskippers (*Entomacrodus striatus*)

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ABSTRACT

Escape responses are vital for the survival of prey. The high speeds and accelerations needed to evade predators successfully require exerting forces on the environment. Unlike water, terrestrial habitats can vary in ways that constrain the forces applied, requiring animals to adjust their behavior in response to variable conditions. We evaluated the terrestrial jumping of an amphibious fish, the blackspotted rockskipper (*Entomacrodus striatus*), to determine if substrate roughness and wetness influence jumping performance. We predicted that rockskippers would produce a greater force output as substrate roughness increased and wetness decreased. Using a novel waterproof force plate capable of detecting millinewton loads, we collected ground reaction forces from rockskippers jumping on wet and dry sandpapers of varying grits. We also used micro-CT scans to quantify muscle mass as a relative fraction of body mass to determine if these jumps could be performed without power amplification. Mixed-model analysis of jumps revealed significantly higher maximum horizontal forces, jump duration, and maximum power on dry versus wet substrates, but no effect of substrate roughness. However, the final jump outcomes (takeoff speed and angle) were unaffected. Peak jump power was within the range of typical fish muscle. Thus, these fish display a jumping behavior which is robust to substrate property variation.

1 | Introduction

Escape responses are a fundamental aspect of animal survival, enabling prey species to evade predators and enhance their chances of survival (O'Steen, Cullum, and Bennett 2002). These behaviors often involve high accelerations, rapid turns, or both, requiring animals to exert high forces on the environment (Howland 1974; Jindrich and Full 1999; Whitford et al. 2019; Wilson et al. 2020). One escape behavior commonly observed in aquatic environments is the C-start response, characterized by rapid body bending followed by a sudden extension (Borazjani 2013; Domenici and Blake 1997; Tytell and Lauder 2008). This maneuver allows high acceleration and rapid direction change to evade predators (Domenici and Blake 1997; Sealer and Binkowski 1988). Fish using a C-start must impart high momentum to the surrounding water, generating enough propulsion to rotate and accelerate the fish while overcoming hydrodynamic drag (Witt, Wen, and Lauder 2015).

Some amphibious fish species evolved dynamic jumping behaviors to move and escape predators on land (Dickinson et al. 2000; Hsieh 2010). In contrast to aquatic environments,

Summary

- The blackspotted rockskipper, *Entomacrodus striatus* performs vigorous jumps with multiple rotations in air.
- Surface wetness is negatively correlated with jump power production.
- We found no evidence of power amplification.

terrestrial movements require interacting with a discrete surface with variable friction and wetness. Consequently, the regulation of forces on substrates is crucial to prevent slipping, potentially causing energy loss (Gamel, Pinti, and Astley 2024a) and reduced performance in amphibious fish lacking specialized foot structures to manage substrate interactions.

The blackspotted rockskipper (*Entomacrodus striatus* (*E. striatus*)), an amphibious combtooth blenny from the Blenniidae family, relies on dynamic jumping as a primary escape mechanism to evade predators in the challenging terrain of intertidal zones. These zones offer a diverse array of substrates, from dry to wet, including algae-covered rocks, among which the fish must adeptly navigate (Aronson 1971; Davenport and Woolmington 1981; Hsieh 2010; Hundt et al. 2014; Heflin, Young, and Londraville 2009; Hixon and Randall 2019; Platt, Fowler, and Ord 2016). While the biomechanics of jumping in other amphibious fishes have been the subject of prior research (Brunt et al. 2016; Gibb, Ashley-Ross, and Hsieh 2013; Hsieh 2010; Lutek, Donatelli, and Standen 2022; Swanson and Gibb 2004; Turko et al. 2017, 2022), the specific influence of substrate properties on the terrestrial jumping performance of fish like the blackspotted rockskipper has not been explored. Understanding how substrate affects performance is vital for revealing the adaptive strategies these species employ in their ecologically complex intertidal habitats.

Previous studies on amphibious locomotion suggest that rougher surfaces may increase frictional force, providing more effective interlocking between the substrate and the animal's body, thus improving grip and reducing the likelihood of slippage (Federle 2006; Bullock and Federle 2011). This enhanced grip could allow animals to exert greater forces during locomotion, crucial for generating the necessary acceleration in escape responses (Autumn et al. 2006). Additionally, dry surfaces tend to maintain higher static friction compared to wet surfaces, which can lower the risk of slipping and provide more consistent force application during a jump (Ditsche, Wainwright, and Summers 2014). Understanding how *E. striatus* and other amphibious species interact with their environment during a jump is crucial to understanding the mechanics of their escape response and the environmental challenges imposed when transitioning from water to land (Axlid et al. 2023). Since rockskippers can launch themselves several body lengths, this suggests they can exert high forces against the substrate, but high forces mean that failures such as slipping impose higher costs in terms of performance or undesirable motion (e.g., spinning) (Bayley, Sutton, and Burrows 2012; Sutton and Burrows 2010; Goode and Sutton 2023; Clemente et al. 2017). Given their small body size, power amplification may play a role in jump mechanics (Ilton et al. 2018). Swanson and Gibb (2004) suggested the possibility of power amplification in another tropical amphibious species, the barred mudskipper, *Periophthalmus argentilineatus* (*P. argentilineatus*).

We hypothesized that increased friction and stability on rougher and drier substrates enhanced the jumping performance of blackspotted rockskippers. To explore this, we directly measured substrate reaction forces in three axes across substrates with differing wetness and roughness and evaluated power amplification based on those measurements and μCT scans of muscle mass. This research aims to explore the critical interplay between environmental factors and escape responses in amphibious species, with implications for understanding ecological adaptations and biomechanical strategies.

2 | Methods

2.1 | Animal Collection and Measurements

Blackspotted rockskippers ($n = 27$) were collected with dip nets from White House Reef (17.49536° S, 149.8512° W) or tide pools on Temae Beach (17.49668° S, 149.756° W), Moorea, French Polynesia. Rockskipper total length was 72.51 mm ± 1.82 (range = 40–97 mm) and a wet mass of 5.13 g ± 2.66 (range = 1.2–13 g).

Fish were collected in the evening and housed overnight (~12 h) with 5–7 conspecifics at the Centre de Recherches Insulaires et Observatoire de l'Environnement CRIOBE: Moorea, French Polynesia, (17.5187° S, 149.8498° W) in aerated seawater aquaria, prior to trials beginning the following morning. Before trials, each rockskipper was weighed and measured for standard length (distance from the snout to the base of the tail). Rockskippers were housed individually in an aerated tank before jumping data were collected. Once trials concluded, the fish were released later the same day at the collection location. Fish were collected, and the experimental protocol was approved via permit #390 issued on May 1, 2023, by the Minister of Culture, Environment, and Marine Resources for the government of French Polynesia.

2.2 | Jumping Trials

Rockskippers were acclimated to the force platform (described below) and landing tank, as they were more inclined to jump after determining a safe area to land (Buo et al. 2020). The landing tank measured 40 × 100 cm, was immediately under the force plate, and was filled with seawater to a depth between 27 and 30 cm. To ensure the experimental conditions closely mirrored the natural habitat of the rockskippers, the housing tanks and experiments were maintained at outdoor ambient temperature, resulting in water temperatures ranging from 22.5°C to 28.2°C, akin to what they would experience in the wild. In our analysis, temperature was tested as a covariate to determine its impact on jumping performance; however, we found it had no significant effect. Rockskippers jumped off a platform (10 cm × 10 cm). Sandpapers (p120 and p2500) (Boshcraft, Duluth, Minnesota, USA) were used as platform substrates and assessed in wet and dry conditions. Wet substrate was achieved by spraying the substrate with seawater until a thin film formed over the sandpaper.

To accommodate the rockskippers' tendency to jump unpredictably in unfamiliar environments (Buo et al. 2020), we surrounded the experimental setup with a white sheet to safely catch any fish missing the landing tank. For acclimation, rockskippers were placed on the force plate adjacent to the water. Each fish was allowed to enter the water twice, voluntarily or with gentle prodding, followed by a 3-min rest between each entry to ensure comfort with the setup (Brunt et al. 2016). The jumping trials commenced after a subsequent 5-min rest in their individual holding tanks.

During the trials, rockskippers were positioned on different substrates in a randomized sequence, where they typically jumped immediately upon placement on the force plate. If a rockskipper hesitated, a gentle prod from behind encouraged the jump, with a failure designated if the fish remained immobile for more than 20 s or moved off the force plate without achieving upward motion (Gibb, Ashley-Ross, and Hsieh 2013). Each fish attempted three jumps per substrate with 3 min of rest between each jump (Hammer 1995) before a 40-min rest in their holding tanks. This rest period was critical for minimizing stress before they underwent the subsequent 12 jumps across the 4 substrate conditions.

Out of all attempts, we prioritized analysis on the jump with the highest force output when a rockskipper successfully jumped more than once under identical conditions. From the collected data, 168 trials were classified as failures due to lack of movement or incorrect execution. An incorrect execution was defined as any trial where the fish failed to launch upward, either remaining stationary or moving laterally off the platform without achieving sufficient vertical motion. An additional 165 trials were excluded due to external disruptions, such as weather conditions affecting sensor accuracy or fish not making full contact with the force plate. For each fish and substrate condition, only the jump with the highest force output was selected for detailed analysis to focus on peak performance and ensure consistency.

2.3 | Force sensing

We quantified the jumping forces of rockskippers on four substrate conditions using a custom 3-axis waterproof force plate capable of detecting forces < 2mN (Gamel, Pinti, and Astley 2024b) (Figure 1). The force plate used in this experiment was modified from Gamel, Pinti, and Astley (2024b) by reducing the thickness of each load cell to increase sensitivity and altering the order of load cells to decrease torsional strain. Load cells were 3D-printed on a Form2 SLA resin printer using Tough 2000 gray resin at 100% infill (Formlab Inc, Sommerville, Massachusetts, USA). Six strain gauges were strategically placed on these load cells on their thinnest sections (Figure 1) with two strain gauges for each load cell. As the rockskippers jumped, their forces would cause deformation in the load cells, which were detected by the stain gauges and recorded as a change in voltage. These pairs of strain gauges were connected in a Wheatstone bridge configuration and further amplified for clearer analysis with an INA125P amplifier integrated into a custom-designed circuit (Gamel, Pinti, and Astley 2024b). To ensure the accuracy of our force measurements, calibrations were performed on-site with weight covering the expected force range (2-, 10-, and 20-gram weights). These weights were used to apply forces in six directions to obtain voltages corresponding to known weights (Biewener and Full 1992; Gamel et al. 2024). This data were organized onto a spreadsheet and loaded to MATLAB to generate a 3 × 3 calibration matrix using thelinsolve function (MathWorks Inc, Natick, Massachusetts, USA). The voltages recorded during trials from rockskipper jumps were multiplied by this calibration matrix to convert the data from voltages to forces. Data were sampled using a NIDAQ USB-6002 (National Instruments, Austin, Texas, USA) at 1000 Hz. Forces were recorded in the vertical, fore-aft, and medio-lateral axes also known as *XYZ* coordinate system. Post-collection filtering was conducted in Python using a Savitzky-Golay filter (signal savgol_filter function with a window_length = 6 and a polyorder = 3 (SciPy, Python)) which filtered out background noise.

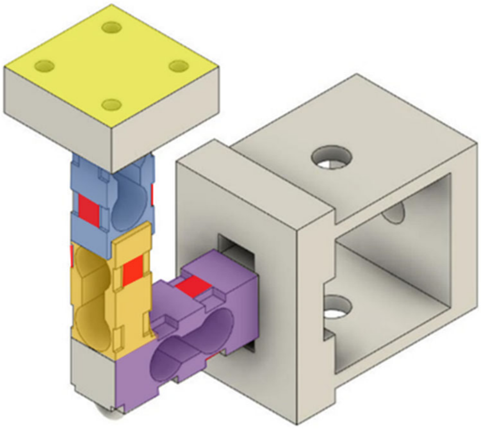

FIGURE 1 | Image of the load cell used to collect force data. The superior section connects to the substrate (yellow), followed by three load cells that measure fore-aft (blue), medio-lateral (orange), and vertical (purple) forces, as seen from top to bottom. Strain gauges were glued to each load cell (red) to detect deformation. The last section attaches this sensor to 80/20 brand extruded aluminum structure to hold the force plate in place.

2.4 | High-Speed Video

We obtained six high-speed videos capturing the movements of rockskippers jumping off a rough substrate. These recordings were taken using a Fastec IL-5q camera (Fastec Imaging Corporation, San Diego, California, USA) brought for another experiment. Videos were recorded at a resolution of 1280 × 1014 at a frame rate of 1000 frames/s. Video recording was conducted independently after completing our primary data collection on a limited number of individuals. The videos were not analyzed for biomechanics but provided a visual record of the fish's behavior at distinct phases of the jumps.

2.5 | CT Scans

Diffusible iodine-based contrast-enhanced computed tomography (diceCT) was performed on 3 formalin-fixed and 1.25%

potassium triiodide-stained fish using a SkyScan 1172 Micro CT Scanner (Gignac et al. 2016) to determine muscle mass compared to overall body mass to calculate power output for rockskipper jumps. Staining was done over 90 h before fish were placed vertically in a plastic tube on the sample holder and scanned at a resolution of 19 µm (voxel size), with a step of 0.4° for a total rotation angle of 180°, and with 8 frames averaging per step. The X-ray source was set to 80 kV, 250 µA, and 10 W. Images taken of epaxial and hypaxial bilateral muscle were rendered and analyzed with VGstudioMAX (VG) (Version 2022.4 for Windows; Hexagon Manufacturing Intelligence Inc., Charlotte, North Carolina, USA).

To account for shrinkage in the scanned rockskippers, a linear regression with the weights and lengths of all rockskippers collected was used to predict the live weight of each formalin-fixed fish, assuming length did not change. We assumed the overall shrinkage of the three specimens scanned (5.4, 13.6, and 14.3%) represents muscle shrinkage and estimated live muscle mass by dividing the scanned muscle mass by the percent of total mass.

2.6 | Calculations

Mass, length, force, and percent muscle mass were used to calculate several variables in Python. Acceleration (m/s^2) was calculated by dividing force (N) by mass (kg) in each of the three axes after subtracting bodyweight from the vertical force. Acceleration was integrated using the trapz function (SciPy, Python 3) and divided by 1000 (sample rate) to get velocity (m/s). Velocity was similarly integrated to get position. Jump angle was calculated as the arctangent of vertical divided by horizontal final velocity. Mass was multiplied by 0.5 and total velocity squared to calculate kinetic energy (reported in mJ). Potential energy (mJ) was calculated by multiplying the mass by gravity ($9.81\ m/s^2$) and by height (vertical position). Total energy (mJ) was calculated as the sum of potential and kinetic energy. Power (mW) was calculated by using the diff function on total energy and multiplying by 1000. Muscle (kg) was calculated using the body weight (kg) multiplied by the percent of muscle (12%) (see below). Power in $W\ kg^{-1}$ of muscle mass was calculated by dividing maximum power (W) by the muscle mass (kg). Jump duration was calculated as the point at which the rockskipper began upward motion to the last point the rockskipper had contact with the force plate.

Of the variables calculated, the maximum values were analyzed to understand the biomechanical performance of rockskipper defensive jumps: maximum power, maximum work, maximum horizontal force, maximum vertical force, and jump duration. Maximum power provides insight into the peak energy generation capability of the fish. Maximum work quantifies the total energy output across the jump, reflecting the overall effort expended. Maximum horizontal and maximum vertical forces reveal the directional strength the rockskipper applies. Lastly, jump duration measures the time taken to leave the force plate from the initiation of a jump, indicating how much time is required to initiate a defensive jump. These variables were selected to capture the essential aspects of jumping dynamics, offering a comprehensive view of the rockskipper's locomotive strategy in response to environmental challenges. While calculated, other metrics like acceleration, velocity, and total energy were not analyzed as they are transformations of other analyzed variables and would have the same significance as those analyzed.

2.7 | Statistical Analysis

Rockskipper jumping data were analyzed with mixed-model ANCOVA using rockskipper identity as the random factor and wetness, roughness, and their interaction as fixed factors. Rockskipper mass was incorporated as a covariate to address size differences. Each performance metric (takeoff angle, maximum power, maximum work, maximum horizontal force, maximum vertical force, and jump duration) served as a separate dependent variable in individual ANCOVA models. Rockskipper identity was included as a random factor to account for repeated measures from the same individuals. Rockskipper mass was incorporated as a covariate to control for size differences among individuals. The fixed factors in our models were substrate wetness and roughness, allowing us to examine their influence on each aspect of jumping performance independently. Additionally, to ensure that the exclusion of trials (due to incorrect execution or external disruptions) did not bias our findings, we performed a series of one-way ANOVAs for each performance metric (takeoff angle, maximum power, maximum work, maximum horizontal force, maximum vertical force, and jump duration) to compare observations that were included to those that were not. These ANOVAs used "included/excluded" as a single, fixed factor to compare trials that were included versus those that were excluded. A nonsignificant p value indicated no difference among groups across these variables. All statistical analyses were performed using Minitab statistical software (Minitab 17, Minitab, State College, Pennsylvania, USA).

We tested the homogeneity of variance assumption of ANCOVA using Levene's Tests (all $p > 0.05$) and the normal distribution of residuals assumption of ANCOVA using Ryan–Joiner Tests. The residuals of all analyses, except for those of the analysis examining takeoff angle, were not normally distributed (all $p < 0.05$). Log transformations of maximum power, maximum work, maximum vertical force, and maximum horizontal force resulted in significantly normal distributions of residuals (all $p > 0.05$). Jump duration violated the normality assumption even with data transformation ($p < 0.05$), but linear mixed-effects models are robust to violations of this assumption (Schielzeth et al. 2020), so we proceeded with this analysis. We tested the homogeneity of regression slopes assumption of ANCOVA by verifying that there were no significant interactions between our independent variables and mass (all $p > 0.05$).

3 | Results

Rockskippers showed impressive jumping ability, with peak horizontal force average across all jumps of 77.39 mN (range = 12.64–286 mN), peak power average of 74.50 mW (range = 12.0–209 mW), and takeoff velocity average of 0.75 (m/s) (range = 0.11–2.95 (m/s)). Maximum horizontal force and maximum power differed significantly based on wetness, with higher values on dry substrates compared to wet substrates (Tables 1 and 2). Jump duration was also longer on dry substrates, indicating that while more force was generated, the jumps took longer to execute. No measures resulted in statistically significant differences based on roughness (Table 2). Additionally, there was no significant interaction of wetness and roughness. There were no significant differences between included and excluded trials across all performance metrics (all $p > 0.05$, Supporting Information), indicating that trial exclusion did not bias our analyses.

Micro-CT analyses estimated ~12% of the rockskippers' total body weight constitutes muscle mass. Subsequent calculation of power (in watts per kg of muscle) revealed that rockskippers are likely not utilizing power amplification to aid in their jumping. On average, across all substrates, rockskipper power

TABLE 1 | Summary of mean values (±1 S.D.) for the six measured variables across the substrate types.

Substrate	Dry rough ($n = 23$)	Dry smooth ($n = 23$)	Wet rough ($n = 20$)	Wet smooth ($n = 17$)
Takeoff angle	47.72 ± 19	50.68 ± 18	51.84 ± 21	52.18 ± 14
Max power (milliwatts)	73.28 ± 37	83.03 ± 54	65.74 ± 40	64.41 ± 42
Max work (millijoules)	2.85 ± 1.6	3.71 ± 3.2	2.51 ± 2.3	2.29 ± 2.0
Max horizontal force (millinewtons)	75.34 ± 42	88.52 ± 56	61.81 ± 42	67.31 ± 48
Max vertical force (millinewtons)	115.04 ± 64	121.26 ± 71	109.34 ± 70	120.27 ± 73
Jump duration (milliseconds)	121.42 ± 98	153.95 ± 106	114.16 ± 77	106.84 ± 76

TABLE 2 | Summary of analysis of covariance (ANCOVA) for blackspotted rockskipper jumping performance.

Response	Fixed effect	β	Num df	Den df	F	p
Takeoff angle (degrees)	Wetness	−1.42	1	63.99	0.51	0.476
	Roughness	−0.74	1	61.59	0.14	0.709
	Wetness*Roughness	−0.65	1	61.03	0.11	0.742
	Mass (g)	0.24	1	30.49	0.08	0.783
Max. power (mW)	**Wetness**	**6.82**	**1**	**58.31**	**4.48**	**0.039***
	Roughness	−0.12	1	56.93	0	0.969
	Wetness*Roughness	−3.76	1	56.59	1.41	0.24
	Mass (g)	**27.61**	**1**	**27.36**	**23.77**	**< 0.001***
Max. work (mJ)	Wetness	0.41	1	64.88	3.06	0.085
	Roughness	−0.11	1	62.47	0.22	0.638
	Wetness*Roughness	−0.30	1	61.91	1.68	0.2
	Mass (g)	**1.24**	**1**	**31.30**	**24.99**	**< 0.001***
Max. horizontal force (mN)	**Wetness**	**9.27**	**1**	**59.51**	**4.92**	**0.030***
	Roughness	−2.44	1	57.90	0.35	0.555
	Wetness*Roughness	−1.70	1	57.51	0.17	0.681
	Mass (g)	**27.01**	**1**	**28.13**	**16.58**	**< 0.001***
Max. vertical force (mN)	Wetness	3.39	1	58.15	0.03	0.533
	Roughness	−0.91	1	56.75	0.39	0.865
	Wetness*Roughness	0.07	1	56.40	0	0.99
	Mass (g)	**39.89**	**1**	**27.14**	**17.72**	**< 0.001***
Jump duration (ms)	**Wetness**	**0.02**	**1**	**59.08**	**6.70**	**0.012***
	Roughness	−0.003	1	57.33	0.13	0.715
	Wetness*Roughness	−0.008	1	56.92	0.99	0.323
	Mass (g)	−0.03	1	27.30	4.16	0.051

Note: This table presents standardized beta coefficients (β) as measures of effect size, with wetness and roughness β values representing conditions of dry and rough surfaces, respectively. The analysis evaluates the impact of substrate conditions (wetness, roughness, and their interaction) and rockskipper mass on various biomechanical parameters of jumping performance, including takeoff angle, maximum power, work, horizontal and vertical forces, and jump duration. Statistical significance is denoted by *, and significant effects are in bold.

was measured at 147.28 W kg^{-1} (± 11.65), which falls within the power output of fish muscle (Frith and Blake 1995; Swanson and Gibb 2004) and thus cannot support a claim of power amplification.

Analysis of a typical jump (defined as the trial with the least variance compared to the mean of each performance measure) revealed that rockskippers have two stages in their jump (Figure 2). High-speed video of jumping shows this first stage (30 ms) as a rapid bending with the support of the pectoral fin to raise the head, followed by an explosive tail flip generating the forces that allow these fish to launch rapidly (Figure 3). These two behaviors likely correspond to the slight, early rise in horizontal force and the second, more prominent horizontal force peak, respectively.

4 | Discussion

Our results demonstrate that rockskipper jumping performance is robust to variation in substrate wetness and roughness, a

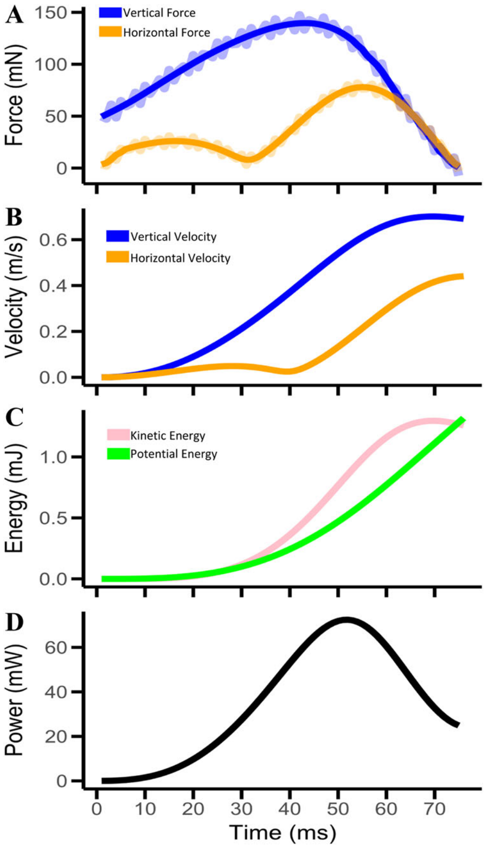

FIGURE 2 | Recorded and calculated values over time for a typical jump of a rockskipper (5.046 g, 7.27 cm). (A) Vertical (blue) and horizontal (orange) forces in millinewtons with the smoothed data superimposed over the raw data. (B) Vertical (blue) and horizontal (orange) velocities in m/s. (C) Kinetic (pink) and potential (green) energies in millijoules. (D) Power (black) in milliwatts.

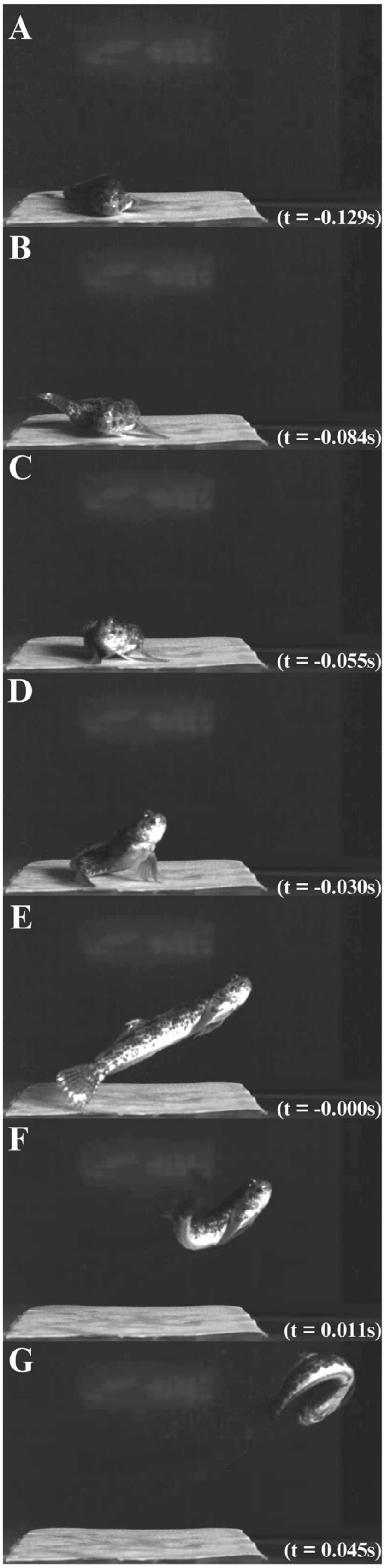

FIGURE 3 | Legend on next page.

finding that aligns with observations in other amphibious fishes (Swanson and Gibb 2004; Hsieh 2010). Although maximum power and horizontal forces were significantly affected by substrate wetness (increasing in dry conditions), work and takeoff angle were not significantly impacted. This suggests that while substrate wetness alters certain aspects of jumping dynamics, the overall jump performance in terms of work done and takeoff trajectory remains consistent. This resilience in performance despite environmental variability is critical for species inhabiting the area between water (Gamel, Pinti, and Astley 2024a) and land, where substrate conditions can change rapidly due to tidal movements (Horn, Martin, and Chotkowski 1998; Hsieh 2010). For instance, mudskippers (*P. argentilineatus*) and mangrove rivulus (*Kryptolebias marmoratus* (*K. marmoratus*)) also demonstrate consistent locomotor performance across different substrate conditions, highlighting a common adaptive strategy among amphibious fishes (Swanson and Gibb 2004; Turko et al. 2022). Furthermore, despite the differences in horizontal force and power, the takeoff velocity and angle remained the same, with only a modest increase in jump duration in wet conditions. However, longer jump durations do not necessarily equate to higher performance. In the context of escape responses, the ability to execute jumps rapidly is often more advantageous for evading predators. Therefore, the observed increase in jump duration on dry substrates may reflect a trade-off between sustained force application and the speed of execution, rather than an enhancement in overall performance. Consequently, despite variations in force and power dynamics, the rockskippers maintained consistent performance in terms of takeoff angle and overall jump execution, albeit with a slightly longer duration in wet conditions. This efficiency in launching behavior underlines their adaptability to varying substrate conditions, which is essential for their survival in the dynamic intertidal ecosystem (Hsieh 2010; Turko et al. 2022).

Performance is also refractory to variation in substrate roughness, as no variables significantly differed between the rough and smooth substrates. The ability of rockskippers to perform similarly across substrates of varying roughness may be attributed to their adhesive capabilities—a trait shared with other intertidal species that navigate both wet and dry conditions (Horn, Martin, and Chotkowski 1998). In rockskippers, adhesion could be facilitated by specialized pelvic fins or ventral skin structures that enhance grip on substrates, similar to mechanisms observed in other blennies (Harris 1960; Hsieh 2010). Observations of rockskippers adhering to steep, wet surfaces in their natural habitat support this possibility (Santos and Castro 2003). Their resilience in wet conditions could also be explained by behavioral adaptations, specifically steep jumping angles that reduce the likelihood of slipping. The angle at which force is applied against the substrate affects the minimum friction coefficient required to prevent slipping. Steeper takeoff angles increase the normal force component relative to the shear force, enhancing frictional resistance and reducing the risk of slippage during the propulsive phase. Although the force angle with respect to the substrate varies throughout the jump, the takeoff angle was typically close to 50° in rockskippers, resulting in an average force angle that is sufficiently steep to maintain friction between their bodies and the substrate—even on smoother or wetter surfaces (Supporting Information). This combination of possible adhesion and behavioral strategies, such as steep jumping angles, likely contributes to their effective locomotion across diverse substrates (Ditsche, Wainwright, and Summers 2014; Persson 2007). Similar findings in northern clingfish, *Gobiesox maeandricus*, which maintain effective adhesion across various rough surfaces, support this explanation (Ditsche, Wainwright, and Summers 2014). By leveraging both morphological adaptations and specific locomotor behaviors, rockskippers can navigate the complex and variable terrains of the intertidal zone successfully.

FIGURE 3 | Still frames from rockskipper jump recorded at 1000 frames a second where 0 s is the point at which the rockskipper leaves the force plate. Times for each panel are given relative to the last instant of contact ($t = 0$, (E)). (A) The rockskipper at rest ($t = -0.129$ s). (B) The tail brought forward in preparation for a jump ($t = -0.084$ s). (C) The tail being pressed back into the plate while the rockskipper raises their body with their pectoral fins ($t = -0.055$ s). (D) The initial extension of the jump ($t = -0.030$ s). (E) The point at which the rockskipper leaves the force plate ($t = 0.000$ s). (F) The rockskipper raising their tail in the air ($t = 0.011$ s). (G) A secondary extension and curling in the air ($t = 0.045$ s).

This robustness to the substrate conditions tested may permit rockskippers to execute jumps effectively across a wide range of encountered substrates in their habitat, which is pivotal for survival. Their habitat, observed to comprise wave-washed rocks ranging from dry, bare surfaces to slippery algae-covered areas (Brainard et al. 2023), highlights the need for a versatile response. Notably, our findings illustrate their adeptness in navigating diverse substrates without compromising performance, reinforcing that jump angle plays a vital role in their adaptive strategy.

While robustness increases the chances of executing a successful jump, rockskippers exhibit another tactic that may provide advantages in escaping predation: their remarkable variability in response to potential threats. Even when given time to familiarize themselves with the tank's position relative to the force plate, rockskippers jumped beyond its boundaries at unexpected angles. In less confined systems, their directional variability was extremely high. This variability in evasive actions parallels the strategies observed in other amphibious fishes such as *K. marmoratus*, which employs unpredictable jumping patterns to evade predators on land (Turko et al. 2022). Such behavioral plasticity is crucial for survival in the dynamic and unpredictable intertidal zone, where environmental conditions can shift rapidly, requiring flexible and adaptable locomotor strategies (Bressman et al. 2019).

While the performances observed in this study are impressive, true maximum trials can prove elusive without collecting large amounts of data (Astley et al. 2013). An interesting observation occurred during an acclimation phase without force plate recording: a rockskipper executed a jump surpassing any measured during the formal trials. The rockskipper was able to jump just above our setup (70 cm above the force plate) and landed just outside of the far side of the tank (110 cm away from the force plate), a feat far greater than any jump recorded during trials. With these values, we calculated the minimum takeoff velocity to achieve that distance of 3.98 m/s (Supporting

Information), which was ~4.5 times greater than the mean takeoff velocity. This exceptional jump performance was also observed in the field during collection, particularly in cases where researchers were not actively attempting to catch them. Such observations suggest that rockskippers may be able to significantly modulate their jumping performance based on context, potentially employing longer, more powerful jumps for purposes such as relocation or navigating their complex intertidal habitats. However, we do not believe this undermines our results, as the slip angle at a given friction coefficient does not depend on force applied, thus, if the rockskippers would slip at too shallow of an angle, this would be true regardless of force.

Rockskippers produced a peak mechanical power output of $147.28\,\mathrm{W\,kg^{-1}}$ muscle mass, which is significantly lower than that observed in species adapted to more terrestrial environments. For instance, the barred mudskipper (*P. argentilineatus*), which exhibits both aquatic and terrestrial locomotion, generates $350\text{–}770\,\mathrm{W\,kg^{-1}}$ muscle mass, aided by power amplification mechanisms (Swanson and Gibb 2004). This suggests that these fish could perform these jumps without power amplification, though it is possible for power-amplified systems to show submaximal performance, even within the scope of muscle power alone (Astley and Roberts 2012). This disparity suggests that rockskippers rely on direct muscle power rather than elastic energy storage systems common in species facing greater terrestrial demands, such as mudskippers and *Alticus* (Hsieh 2010; Ilton et al. 2018). The lack of power amplification in rockskippers likely reflects the ecological pressures they encounter as rapid, short bursts of power are sufficient for survival in the intertidal zone.

When compared to other amphibious species, such as mudskippers (*P. argentilineatus*) and mangrove rivulus (*K. marmoratus*), the jumping mechanics of *E. striatus* demonstrate key similarities and distinctions. Mudskippers perform prone jumps using coordinated pectoral fin and body movements to enhance stability and power during takeoff (Swanson and Gibb 2004). In contrast, *Kryptolebias* employs tail-flip jumps, characterized by a rapid tail flick that generates propulsion and lift, often accompanied by significant rotational motion (Gibb, Ashley-Ross, and Hsieh 2013). Like mudskippers, rockskippers also utilize a prone jump strategy, but without signs of power amplification mechanisms.

High-speed video analysis revealed that rockskippers execute a two-phase prone jump, similar to mudskippers. In the first phase, rockskippers lift their head and anterior body with their pectoral fins, preparing for the propulsive phase (Figure 3, $t = -0.055$ s), a movement that may also enhance substrate adhesion and stability. The second phase involves rapid body and tail extension, generating the propulsive force needed for takeoff (Figure 3, $t = -0.030$ s). This coordinated movement of the pectoral fins and axial musculature contributes to controlled takeoff angles and precise trajectories, enabling effective navigation through complex intertidal terrains (Gibb, Ashley-Ross, and Hsieh 2013; Swanson and Gibb 2004).

By utilizing prone jumps, rockskippers achieve a balance between control and efficiency, well-suited to the intertidal zone's ecological demands, where short bursts of power are crucial for survival. In contrast, tail-flip jumpers like mangrove rivulus (*K. marmoratus*) often exhibit less controlled trajectories due to increased rotational movement (Gibb, Ashley-Ross, and Hsieh 2013; Turko et al. 2022). The controlled takeoff angles in rockskippers allow for precise navigation and obstacle avoidance, while pectoral fin elevation reduces reliance on substrate conditions. This combination contributes to the robustness of their performance across varying wetness and roughness, facilitating their successful locomotion in dynamic intertidal environments.

The force plate (Gamel, Pinti, and Astley 2024b) successfully detected very subtle forces exerted by rockskippers, although its high sensitivity also captured atmospheric disturbances like thunderstorms and nearby construction. The device has potential for further development by enhancing shielding against such disturbances and improving isolation from ground vibrations to reduce background noise. This low-cost, field-ready device represents a significant advancement in the study of amphibious fish locomotion, allowing for the direct measurement of force output in naturalistic settings. By capturing the true center of mass dynamics, it provides insights often obscured in kinematic studies, particularly in species with complex body movements like the rockskipper (Gamel, Pinti, and Astley 2024b). This approach aligns with recent calls in biomechanics for more ecologically valid experimental setups that can reveal the nuanced interactions between an organism and its environment (Dickinson et al. 2000).

Collecting force data allows for the direct calculation of takeoff velocity, work, and power of the true center of mass, regardless of body deformations that dynamically shift the center of mass location. This is particularly important when measuring behaviors like rockskipper jumping, which involves drastic postural changes and postlaunch rotations (Figure 3), potentially introducing artifacts in calculations based on kinematic measurements of proxy points. By providing a novel methodology for capturing the nuanced dynamics of amphibious locomotion, this study sets the stage for future explorations that promise to deepen our understanding of the evolutionary adaptations enabling life to thrive at the water's edge.

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Data Availability Statement

The data that support the findings of this study are openly available in Raw data for Navigating Nature's Terrain: Jumping Performance at https://datadryad.org/stash, reference number DOI: 10.5061/dryad.c59zw3rjk.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.