

## RESEARCH ARTICLE

# Temperature affects susceptibility of intertidal limpets to bird predation

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## ABSTRACT

High temperatures resulting in physiological stress and the reduced ability to resist predation can have life-or-death consequences for an organism. We investigated the effects of temperature on the susceptibility to predation for an ectothermic intertidal mollusc (the owl limpet, *Lottia gigantea*) and its predator (the black oystercatcher, *Haematopus bachmani*). The ability of *L. gigantea* to resist bird predation during low tide is determined by the tenacity of attachment to the rock. We developed a transducer to measure the force of predatory attacks on limpets by a captive black oystercatcher, and tested the hypothesis that exposure to warm temperatures during low tide emersion would affect the limpet's ability to resist dislodgement in trials with a morphometrically accurate beak mimic and a live bird. In beak mimic trials, four times as many limpets exposed to warm low tides were removed, as compared with limpets exposed to cool low tides or in 'no low tide' submerged conditions. Minimum time before limpet removal in captive bird trials was more than six times longer for limpets in cool low tide or no low tide treatments compared with limpets in the warm low tide treatment. We measured shear forces up to 36.63 N during predatory strikes. These direct measurements of the forces exerted by a living oystercatcher provide context for interactions with multiple prey species. Our data suggest that naturally occurring variation in body temperatures among individual prey items in the field could be an important driver of predator-prey interactions and subsequently community patterns.

**KEY WORDS:** *Haematopus bachmani*, Owl limpet, *Lottia gigantea*, Low tide exposure, Black oystercatcher, Tenacity, Thermal history

## INTRODUCTION

For ectothermic organisms, temperature has obvious and well-documented effects on biochemical and physiological rates and thus plays a critical role in the function of individuals (Kordas et al., 2011). Scaling up, these rate effects on individuals can shape important species interactions in predictable ways, as long as the temperatures remain near the center of the target individual's thermal range (Sanford, 2002a). For example, in warm water, temperate sea stars (Sanford, 1999, 2002a,b) and whelks (Sanford, 2002a,b; Miller, 2013) show elevated prey consumption rates

compared with cold water conditions. Yet the effect of temperature on biological systems is often not linear, and numerous aspects of performance are negatively impacted when temperatures cross the threshold from 'optimum' to 'stressful' (Sanford, 2002a). Elevated temperatures in the stressful but non-lethal range can affect the production of (and energy investment in) heat-shock proteins (Hofmann and Somero, 1995; Tomanek, 2002; Dong and Williams, 2011; Miller et al., 2009), cause irreversible damage to (and subsequent breakdown of) cellular proteins (Hofmann and Somero, 1995; Bjelde and Todgham, 2013) and cause damage to or atrophy of muscular proteins (Tomanek and Zuzow, 2010; Serafini et al., 2011; Madeira et al., 2015). Together, these effects could have important implications for muscular control and energy budgets and thus impact the performance of organisms in crucial tasks. For example, impaired muscular function could have life-or-death consequences for an ectothermic prey organism if their ability to escape or resist predation is reduced.

Over the long term, improving our understanding of how stressful environmental conditions influence predator-prey interactions is an important step toward improving our overall ability to generate comprehensive predictions about the effects of climate warming on community structure and function (Kordas et al., 2011). More proximally, addressing this topic gives us important insight into species interactions and their role in structuring communities under current conditions in thermally heterogeneous environments. In the rocky intertidal zone, the body temperatures of ectothermic organisms are generally equivalent to the water temperature during immersion (Helmuth, 1998; Helmuth and Hofmann, 2001; Szathmary et al., 2009). However, during low tide emersion, the body temperatures of ectotherms can be higher than air temperature, as body temperature can be influenced by exposure to solar irradiance, air temperature, wind, angle of substratum and heat exchange with the substratum (Bell, 1995; Helmuth, 1998; Denny and Harley, 2006; Denny et al., 2006; Miller et al., 2009). An organism's microhabitat location (e.g. under canopy algae, in a tide pool or on open rock) can strongly influence body temperatures (Somero, 2002; Tomanek, 2002; Burnaford, 2004; Firth and Williams, 2009; Dong and Williams, 2011; Chaperon et al., 2017; McAfee et al., 2018). Because the rocky intertidal zone is an environment with complex topography and a large number of microhabitats, individuals in close proximity to each other can experience very different temperatures during low tide emersion (Burnaford, 2004; Broitman et al., 2009; Denny et al., 2011; Seabra et al., 2011; Marshall et al., 2013). The degree to which this thermal heterogeneity influences species interactions such as predation is still largely unknown.

In this study, we investigated the effects of prey item body temperature on the susceptibility to predation for an ectothermic intertidal mollusc, the owl limpet (*Lottia gigantea* Sowerby 1834), and its highly mobile endothermic predator, the black oystercatcher (*Haematopus bachmani* Audubon 1838). *Lottia gigantea* are large

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(individuals can exceed 100 mm in length) herbivorous molluscs common in the mid intertidal zone on rocky shores on the west coast of North America from Washington State to Baja California (Morris et al., 1980). *Lottia gigantea* individuals establish and defend territories up to 900 cm<sup>2</sup> and thus strongly affect the diversity and abundance of organisms in this habitat (Stimson, 1970, 1973; Lindberg et al., 1998). *Haematopus bachmani* are found along the North American west coast from the western Aleutian Islands, Alaska to Baja California (Hockey, 1996). These large, mobile consumers forage during low tide and can have substantial impacts on the distribution and abundance of their invertebrate prey items (Hartwick, 1976; Marsh, 1986; Lindberg et al., 1987; Hahn and Denny, 1989). As much as 50% of the *H. bachmani* diet consists of limpets (Webster, 1941a; Hartwick, 1976; Morrell et al., 1979; Lindberg et al., 1987) and *L. gigantea* is a preferred prey item (Lindberg et al., 1987, 1998). The birds use their tapered beak to strike at limpets to dislodge them; after dislodging a limpet from the rocky substratum, the bird will flip the prey item over and remove the flesh, leaving the shell behind.

*Lottia gigantea* forage while washed by waves or at high tide, but are stationary during low tide emersion, when oystercatchers are foraging. Emerged *L. gigantea* clamp their shell tightly against the substratum in response to disturbance, and thus their ability to resist predation by birds during low tide is determined by the tenacity of their attachment to the rock, created by muscular contractions and mucus adhesion of the large muscular foot, which fills up most of the oval shell aperture (Fisher, 1904; Denny and Blanchette, 2000). Based on the large number of documented physiological and cellular effects of elevated temperatures on the muscular performance of ectothermic animals, we hypothesized that exposure to warm temperatures during low tide emersion would affect the ability of *L. gigantea* to resist dislodgement and thus influence their susceptibility to black oystercatcher predation. In the field, we used biomimetic temperature data loggers to characterize *L. gigantea* body temperatures in different microhabitats. We developed a novel force meter to quantify the force exerted by oystercatchers during simulated predation events. We subsequently used these data to develop complementary experiments to rigorously test our hypothesis. We exposed limpets to environmentally relevant temperatures in two different types of experimental trials (live captive oystercatcher and predation mimic) to determine whether limpets exposed to warm low tide temperatures would be more susceptible to oystercatcher predation than limpets exposed to cooler temperatures. This study furthers our understanding of the extent to which temperature affects predator–prey dynamics and therefore the structure of rocky intertidal communities.

## MATERIALS AND METHODS

### Characterization of thermal conditions for limpets in the field

In order to characterize the range of temperatures experienced by owl limpets in the field, we placed ‘robolimpet’ biomimetic temperature loggers (which incorporate iButton Thermocron data loggers, DS1922L-F5#, Maxim Integrated Products, San Jose, CA, USA, hereafter ‘iButtons’; after Lima and Wethey, 2009) on rock surfaces on which we had observed owl limpets at Dana Point, in Orange County, California, USA (33.460079°N, 117.714655°W; Pound, 2017). Briefly, we dissected iButtons to remove circuit boards and batteries from external casings. We used 3M Scotchcast 2130 Flame Retardant Compound (3M, St Paul, MN, USA) to attach data loggers and batteries inside empty *L. gigantea* shells that measured 30–40 mm in length. We placed loggers in four microhabitats in which we had observed owl limpets: flat rock,

and sloped rock surfaces facing north, south and west (Pound, 2017). Two to three loggers per microhabitat type were deployed between June 2014 and June 2016 (Fig. S1; sample size varied over time owing to occasional logger failure). Loggers recorded temperature at 10 min intervals and data were downloaded at approximately 28 day intervals.

We used Navicat for MySQL version 12.0.13 (PremiumSoft™ CyberTech Ltd, Kowloon, Hong Kong) to extract temperatures recorded during periods of low tide emersion at our field site based on verified tidal height data from the NOAA tidal station at the Newport Bay Entrance, Corona del Mar (Station 9410580, 33.6033°N, 117.8830°W). We used these data to extract the highest 10% of low tide temperatures for each logger over the period of deployment and to calculate the mean, standard deviation, maximum and minimum of these warmest temperatures for each physical location (Fig. S2).

### Captive bird maintenance

Captive bird trials were conducted with a resident black oystercatcher (named Squeakers) at the Living Coast Discovery Center (LCDC) in Chula Vista, CA, USA. Squeakers was hatched in 1999 and bred in captivity on a diet of fish. In order to maintain natural beak shape and dimensions, the bird’s beak was trimmed at regular intervals by the facility animal care manager (Fig. S3). Because the bird was naive to the experience of active predation on limpets, we trained him to identify live limpets as potential prey. The bird was transferred to a private enclosure and given a single *L. gigantea* (dorsal/shell side down) on a food dish. After the bird consumed the first limpet, we gave the bird a second *L. gigantea* (dorsal/shell side up), which the bird attacked and consumed. We fed the bird four additional individual *L. gigantea* (dorsal/shell side up) to establish limpets as a food item. To ensure that the bird was accustomed to the set-up for our predation experiments, over six non-consecutive days we presented him with an additional 37 limpets each on an individual clay tile (see ‘Simulated predation trials’ below). The bird attacked and removed each of them. We therefore determined that the bird was sufficiently trained to recognize *L. gigantea* as potential prey.

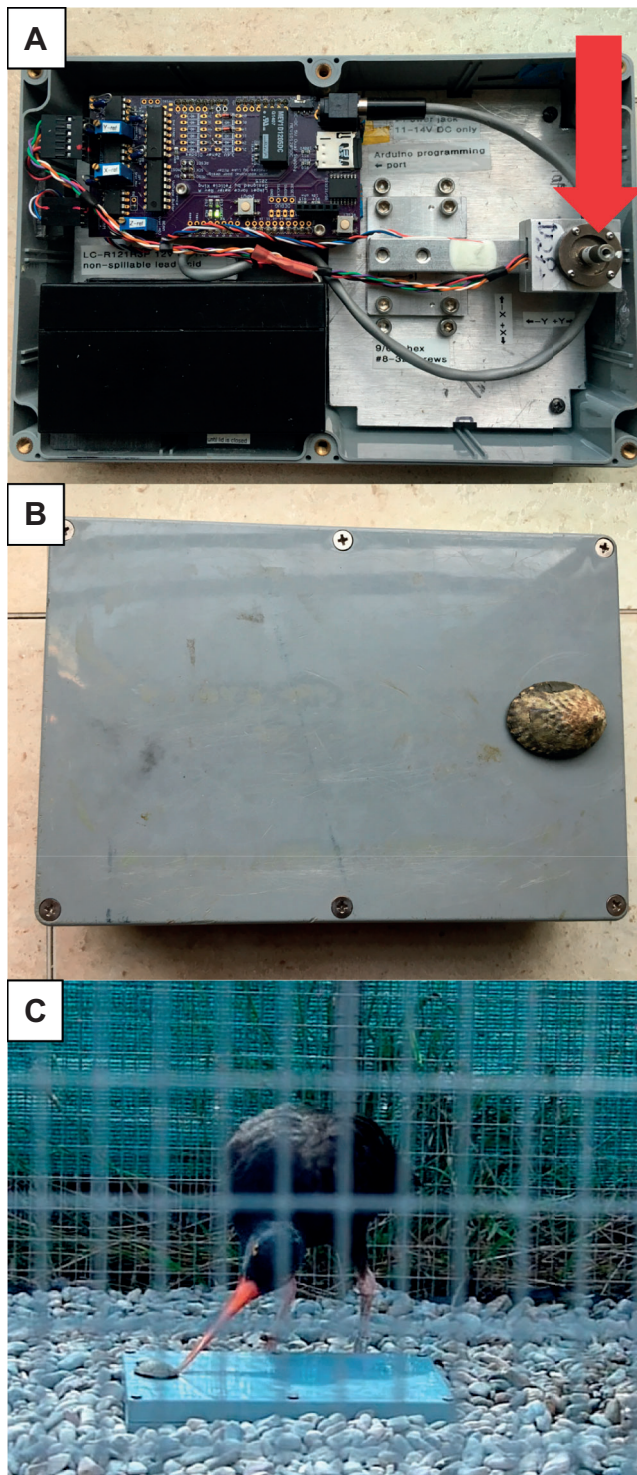
On experimental trial days, the bird was housed alone in a private enclosure and was not provided with a morning meal (to encourage the bird to remove and consume limpets during trials). Force meter trials were typically conducted on the same day as live limpet predation trials, in which the bird was presented with three to six live *L. gigantea* prey items. If trials were planned for subsequent days, the animal care manager would evaluate the number of limpets consumed by the bird and determine whether an evening meal was appropriate (to encourage the bird to remove and consume limpets during subsequent trials).

All field research was conducted in accordance with requirements established by the California Department of Fish and Wildlife (SCP-1286). All trials involving the live captive black oystercatcher were conducted in accordance with requirements established by the CSU Fullerton Institutional Animal Care and Use Committee (IACUC Protocol No. 15-R-01) and California Department of Fish and Wildlife (SCP-1286), in consultation with and under the supervision of the Living Coast Discovery Center animal care manager.

### Measuring the force exerted by a black oystercatcher predator

We built a force meter with an epoxy-filled *L. gigantea* shell acting as a prey mimic to measure the forces (in three dimensions) exerted by a black oystercatcher during predation events (Fig. 1). Our





**Fig. 1. Force meter design.** (A) Internal components. The transducer, which measures force in three dimensions, is indicated by an arrow. (B) External appearance, including owl limpet mimic (attached to transducer below it). (C) Screen shot of a trial with the captive bird.

measurement apparatus was a custom-built three-axis force transducer powered and sampled using an Arduino Due microcontroller (<http://arduino.cc>). The three-axis transducer setup comprised a two-axis (horizontal  $x$ - and  $y$ -axes, Bokam Engineering US-series, Santa Ana, CA, USA) transducer mounted on a single-axis load cell transducer (vertical  $z$ -axis, Uxcell 0–1 kg, Kwai Fong,

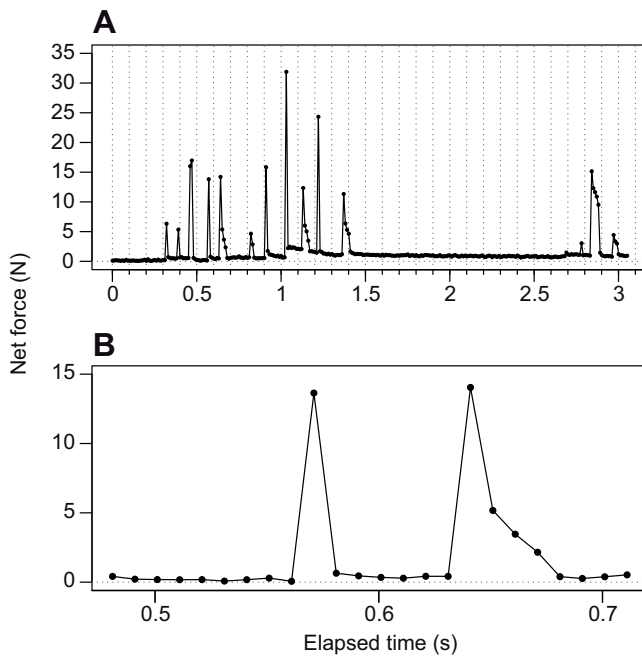
Hong Kong). All three transducers used strain gages arranged in a Wheatstone bridge configuration, powered by a  $\pm 5$  V supply. Output signals were amplified by AD620 instrumentation amplifiers (Analog Devices, San Jose, CA, USA) configured for  $8.2\times$  gain on the horizontal axes and  $16\times$  gain on the vertical axis. The amplified signal was inverted by LM324 operational amplifiers (Texas Instruments, Dallas, TX, USA) configured as unity gain amplifiers and low-pass filters with a 482 Hz cutoff. The Arduino Due analog-to-digital converters recorded each transducer channel at an effective resolution of 12 bits for a resolution of 0.8 mV on the microcontroller's 3.3 V supply voltage, yielding a resolution of 0.05 N on the horizontal axes and 0.06 N on the vertical axis. Each axis was calibrated separately by hanging known masses off the end of a 0.58 cm length screw threaded into the top of the force transducer. The apparatus sampled all three axes at 100 Hz in 5-min bursts and wrote the data to a micro SD card along with timestamps. We used the timestamps to align transducer data with video recordings of the focal oystercatcher during trials. Using the separate calibration regressions for each transducer axis, we converted raw transducer output voltages into equivalent force on each axis. The net force ( $F$ ) was calculated as the three-dimensional Euclidean norm of the forces on the horizontal axes ( $x$  and  $y$ ) and vertical axis ( $z$ ):

$$F = \sqrt{x^2 + y^2 + z^2}. \quad (1)$$

The force transducer was housed in a plastic case, with the top of the force transducer post protruding through a hole in the case top. A *L. gigantea* shell (length=36 mm, width=26 mm, height=9 mm) was filled with epoxy to secure a threaded rod that emerged from the bottom of the shell. The shell could be screwed into the top of the force transducer post so that the epoxy-filled shell sat nearly flush with the top of the force transducer case, leaving a small (2–3 mm) gap so that the shell would not contact the case when the oystercatcher manipulated the shell.

We presented the force meter to the captive black oystercatcher in six trials over 8 months, with a maximum of one trial per day. A force meter trial began when we placed the force meter in the bird's enclosure and immediately exited the enclosure. During each trial, the bird had the option to attack or ignore the device. We filmed each trial at 120 frames  $s^{-1}$  using a high-speed video camera (Panasonic Lumix DMC-FZ200), located directly outside of the bird's enclosure. A trial was considered to be complete 5 min after the bird started interacting with the force meter, or if there was no interaction, 30 min after the placement of the force meter. The bird interacted with the force meter for a total of 64.23 s (3.88 to 18.73 s on any single day).

The force meter recorded data at 10 ms intervals. Each sampled data point during which any net force was recorded was considered to be an 'event'. We established three mutually exclusive event definitions based on two parameters: event magnitude and event duration. An event was classified as a 'peck' (Fig. 2) if the magnitude of the peak force was  $\geq 2$  N, greater than or equal to twice the intensity of the net forces that occurred immediately before and after it, and  $\leq 30$  ms in duration (i.e. a single sample or two adjacent samples with forces higher than the 2 N threshold). An event was classified as a 'push' (Fig. 2) if the peak magnitude of net force was  $\geq 2$  N but not greater than or equal to twice the intensity of the force that occurred in the sampling intervals immediately before and after it, or the time interval where net force was  $\geq 2$  N exceeded the 30 ms threshold defined for a peck. A push could last for any length of time



**Fig. 2. Examples of net forces exerted by the captive oystercatcher on the force transducer.** Net force (N) was calculated as the three-dimensional Euclidean norm of the forces recorded by the three axes of the force transducer (see Materials and Methods for further description). (A) Three seconds of data showing a mixture of strikes classified as pecks or pushes. (B) A shorter time interval extracted from the upper panel illustrating two categories of events. The first event ( $t=0.56$  to  $t=0.58$  s) would be classified as a peck with a maximum force of 13.6 N. The second event ( $t=0.63$  to  $t=0.68$  s) would be classified as a push with a maximum force of 14.0 N.

greater than 10 ms. For analysis, we used the maximum net force exerted during any single peck or push event. When the magnitude of net force was  $<2$  N, the event was classified as a ‘touch’. Because direct observations indicated that recordings classified as ‘touches’ typically corresponded to behavior that appeared to be exploratory (e.g. pulling on the limpet mimic) rather than predatory, we did not include touches in our analyses.

We converted raw transducer outputs to equivalent forces for each axis and calculated the net forces for each event. We used R v3.5.1 (<https://www.r-project.org/>) to calculate the overall maximum, minimum, mean and standard deviation of the force as well as the mean of the top 10% of the greatest net forces, for push and peck events.

### Simulated predation trials

We designed a mimic for a black oystercatcher beak (hereafter ‘beak mimic’) using morphometric measurements of 13 black oystercatcher specimens (five males and eight females) from the Natural History Museum of Los Angeles County. Beak mimic dimensions were set to mean values of the 13 specimens for five beak dimensions: length (69.0 mm), depth at base (15.5 mm), depth at tip (6.3 mm), width at base (13.9 mm) and width at tip (1.6 mm).

Beak mimics were designed using Autodesk 123D Design version 94.1.6 (Autodesk, Inc., San Rafael, CA, USA) and printed from base to tip using a 3D printer (Orion Delta Desktop 3D Printer RTP3D printer, SeeMeCNC, Goshen, IN, USA) with 1.75 mm Light Blue PLA 3D Printer filament (SeeMeCNC). In order to ensure the beaks could withstand repeated exposure to 14 N of force, we conducted mechanical compression tests on beak mimics to 60 N. Compression tests were completed using a materials-testing

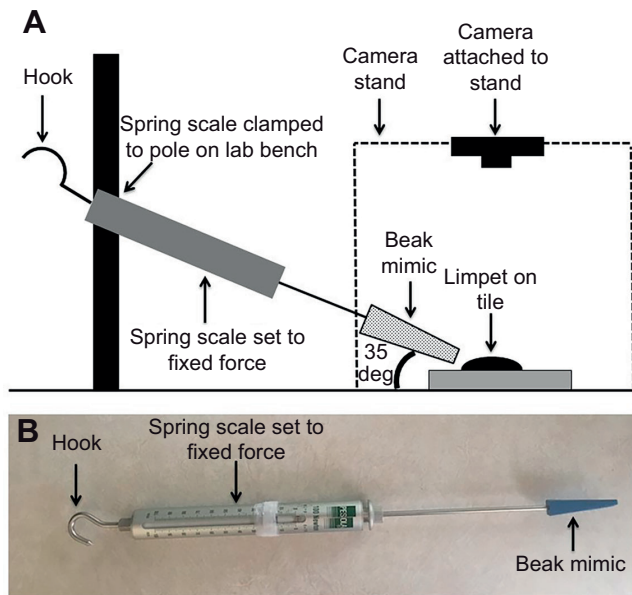
system (Single Column Table Top Systems, Model 5942, Instron, Norwood, MA, USA) and corresponding testing software (Bluehill 3 software, Instron), using a 50 N load cell, at room temperature and humidity. The compressive load was applied lengthwise on the beak (beak base to beak tip) until the maximum force of the load cell was reached (60 N, approximately four times greater than that in simulated bird predation trials). We tested three beak mimics in total and visually inspected a subset of beak mimics after mechanical compression to confirm that they showed no signs of deformation or cracking. The beak mimic used in our laboratory studies did not undergo compression testing. We used calipers to measure dimensions of beak mimics before and after each simulated bird predation trial, and no changes in dimensions were detected.

We collected *L. gigantea* 30–40 mm in length from Newport Jetty (Orange County, CA, USA) and White Point Beach (San Pedro, CA, USA) 1 day before they were used in a trial. The timing of dislodgement relative to measurement of stationary tensile tenacity is similar to Denny and Blanchette (2000) (1–2 days; Mark W. Denny, Stanford University, personal communication). Limpets were transported to CSU Fullerton in chilled aerated seawater (mean  $\pm$  s.d. =  $12.83 \pm 0.56^\circ\text{C}$ ,  $N=138$  readings over 2 days, measured at 1 min intervals with iButton Thermocron data loggers). At CSU Fullerton, individual limpets were placed on separate  $15.2 \times 15.2$  cm unglazed clay tiles (Quarry Textures Diablo Red 0T01, Daltile, Dallas, TX, USA). Tiles standardized heat conduction and surface characteristics (e.g. rugosity) and allowed us to move individual limpets among treatments with minimal disturbance. Limpets were held under simulated high tide conditions in coolers with aerated seawater (mean  $\pm$  s.d. temperature =  $15.82 \pm 0.51^\circ\text{C}$ ,  $N=411$  readings over 30 trials, measured at 5 min intervals with iButton data loggers) for 14.5 to 17.3 h prior to experimental treatments. We temporarily placed a 7 cm tall fence of black vexas mesh (1/4 inch mesh size, Memphis Net and Twine, Memphis, TN, USA) around each tile to prevent limpets from moving off of tiles during submersion.

After the simulated high tide, individual limpets (on individual tiles still surrounded by fences) were randomly assigned to an experimental treatment. Limpet shell lengths did not differ among experimental treatments (ANOVA on raw data:  $F_{2,27}=1.26$ ,  $P=0.3$ ). The duration of the experiment was set at 4 h to approximate low tide exposure times in Newport Beach, California (based on the calculated mean low tide exposure time at 0.3 m above MLLW in June 2014; [www.noaa.gov](http://www.noaa.gov)). We placed a single iButton data logger on the tile next to each limpet to record temperatures during experimental treatments. We established three treatments. In the no low tide (NLT) treatment, limpets were maintained on their individual tiles in aerated seawater (overall mean  $\pm$  s.d. temperature =  $15.56 \pm 0.17^\circ\text{C}$ ,  $N=2409$  readings). In the cool low tide (CLT) and warm low tide (WLT) treatments, limpets were maintained on their individual tiles out of water. We manipulated air temperature in the CLT treatment to lower limpet body temperatures (ice packs were placed near the limpets on an insulated surface: CLT overall mean  $\pm$  s.d. temperature =  $13.94 \pm 0.40^\circ\text{C}$ ,  $N=2407$  readings). We used heat lamps in the WLT treatment to elevate body temperatures (overall mean  $\pm$  s.d. temperature =  $29.73 \pm 0.39^\circ\text{C}$ ,  $N=2408$  readings). Limpets were exposed individually on their individual tiles to the appropriate experimental treatment, with start times staggered by 9 min so that immediately upon the conclusion of the 4-h treatment, the limpet was exposed to a simulated predation event. Treatment start times and the order in which we tested limpets were determined randomly.

To simulate a bird predation event, we used a force gauge (after Hahn and Denny, 1989; Fig. 3) to apply a standard amount of





**Fig. 3. Experimental set-up for the simulated bird predation trials.** (A) Experimental set-up depicting use of beak mimic to simulate predatory strikes. (B) The bird mimic consists of a 100 N spring scale and beak mimic printed using a 3D printer using beak dimensions calculated from measurements of museum specimens.

compressive force to the edge of the limpet shell at a standard angle. Our ‘bird mimic’ was constructed by attaching the beak mimic to the end of the stainless-steel rod of a calibrated spring scale modified into a pressure/force gauge (Pressure Set for Macro-Line with a Macro-Line Spring Scale 100 N, Pesola, Schindellegi, Switzerland).

To start a simulated predation trial, we removed the mesh fence around a tile, secured the tile to the lab bench using spring clamps (3 inch Metal Spring Clamp with Pivot Tips, Husky, Atlanta, GA, USA), and gently tapped the limpet five times on the apex to standardize attachment (after Denny and Blanchette, 2000). To deliver a predatory strike, we used the hook to pull the spring scale a fixed distance to administer a fixed force with the beak mimic. Our observations of a captive black oystercatcher attacking real limpets (see ‘Captive bird predation trials’, below) indicated that successful strikes (defined as a strike in which the bird dislodged the limpet) could originate from many different locations on the limpet shell and many different angles. To be consistent in this laboratory study, all strikes were delivered to the anterior edge of the limpet shell at a fixed angle of 35 deg above horizontal. This strike angle was chosen based on preliminary observations of the captive bird during feeding trials.

Our goal was to use a biologically relevant amount of force in simulated predation trials. Preliminary force meter trials with the captive bird indicated that the bird frequently delivered multiple predatory strikes in quick succession and that the strongest force was rarely applied during the first strike. After analyzing preliminary force meter data, we set our simulated predation trials to start with one 3 N strike, followed by up to ten 14 N strikes. Timing between strikes ranged from 20 to 90 s. We tested 10 limpets per experimental treatment. After each strike, two independent observers assessed the position of the limpet relative to its pre-strike position and determined whether the limpet remained attached to the tile or had become detached. If both observers concluded that the limpet had become detached from the tile, the

trial was considered to be complete and no further strikes were applied. If the limpet remained attached to the tile, its location relative to the pre-strike position was noted and recorded as either a ‘slide’ (a lateral move on the tile) or ‘no movement’ before another strike was delivered. Trials were concluded when the limpet was detached or when ten 14 N strikes had been delivered. At the conclusion of each trial, we manually pulled on the limpet shell to confirm our visual classification: detached limpets were easily separated from the tile while attached limpets were not. We photographed limpets before and after each strike using a digital camera (PowerShot SD630 Digital Elph, Canon, Melville, NY, USA) positioned 20.2 cm above the limpet, and we analyzed the photos to quantify the changes in limpet position after each strike (using SketchUp Make version 17.2.2554, Trimble Inc., Sunnyvale, CA, USA). Limpets were returned to ambient temperature seawater following experiments. Observations 24 and 48 h after the experiment confirmed that all tested limpets survived the experimental conditions and treatments.

We considered that limpets that were dislodged from the tile would be susceptible to predation, whereas limpets that were not removed from the tile would be less susceptible. In order to determine whether low tide exposure and temperature affected limpet removal from tiles, we compared the proportions of limpets removed among experimental treatments using the two-sided Fisher’s exact test on raw data (Ramsey and Schafer, 2002).

For the subset of limpets that were removed from tiles, we calculated the mean number of strikes required to remove limpets from each experimental treatment. However, because the number of limpets that were removed by the simulated bird strikes varied among treatments, we did not conduct statistical tests on these data.

### Captive bird predation trials

Methods for *L. gigantea* collection and maintenance for captive bird predation trials are the same as those described above (see ‘Simulated predation trials’) with few exceptions. Limpets for captive bird trials were collected 1 to 2 days prior to a trial, and transported to the LCDC in water with an overall mean±s.d. temperature of 15.56±0.60°C ( $N=357$  readings, measured at 1 min intervals with iButton data loggers). At LCDC, limpets were held on individual tiles surrounded by fences under simulated high tide conditions in coolers with aerated seawater (mean±s.d. temperature=15.70±0.62°C,  $N=6591$  readings over 27 trials, measured at 1 min intervals with iButton data loggers) for 15.12 to 40.13 h prior to experimental treatments.

After the simulated high tide, individual limpets (on individual tiles still surrounded by fences) were randomly assigned to an experimental treatment of 4 h duration. Limpet shell lengths did not differ among experimental treatments (ANOVA on raw data:  $F_{2,24}=0.21$ ,  $P=0.81$ ). Our three treatments were the same as for simulated predation trials, with only slight differences in temperature: no low tide (NLT) treatment, overall mean±s.d.=16.35±0.25°C,  $N=2156$  readings; cool low tide (CLT) treatment, overall mean±s.d.=16.54±0.54°C,  $N=2162$  readings; warm low tide (WLT) treatment, overall mean±s.d.=32.05±0.51°C,  $N=2145$  readings.

Three to six limpets were tested on each day, with treatment start times staggered by 35 min. Within 5 min of the conclusion of the 4-h experimental treatment, a limpet was presented to the bird in a 30-min predation trial. The order in which we tested limpets was random with regard to experimental treatments. To start a predation trial, we removed the mesh fence around the tile, gently tapped each limpet five times on the apex to standardize attachment, placed the

tile in the bird's enclosure, and immediately exited. We recorded high-speed video of each trial (120 frames  $s^{-1}$ ; Panasonic Lumix DMC-FZ200, Newark, NJ, USA) from a position outside of the enclosure.

We considered limpets that were removed from the tile to be susceptible to bird predation. During each trial, the bird had the option to ignore the limpet or attack it; the trial was considered to be complete after the bird consumed the limpet flesh or 30 min after tile placement. We tested nine limpets per treatment. Limpets that were removed by being pushed off the edge of the tile rather than dislodged by the bird were excluded from analyses, leaving a final sample size of eight, seven and nine limpets in the NLT, CLT and WLT treatments, respectively.

To determine whether low tide exposure or temperature affected limpet removal from tiles, we compared the proportion of limpets removed among experimental treatments. We reviewed the video to sum the total interaction time (defined as any time the bird was attacking the limpet until the limpet was removed) and examined the data for outliers using Grubbs' test on raw data (Grubbs, 1950). We compared bird–limpet interaction times among experimental treatments using an ANOVA on ln-transformed data followed by Tukey's honest significant difference (HSD) comparisons.

## RESULTS

Robolimpet temperatures varied among locations over short and long time scales (Figs S1 and S2; Pound, 2017). The highest temperatures varied among microhabitats in subtle but important ways. Maximum recorded temperatures were higher on flat rock and south-facing vertical rock than in other microhabitat types, while mean and minimum temperatures were higher on south-facing vertical rocks than in other microhabitats. High temperature events were not synchronous among habitat types; for example, maximum temperatures recorded on south-facing vertical rock were logged in January (42°C), while the maximum temperatures on north-facing vertical rock were recorded in April (32.5°C). This seasonal temperature pattern is not unusual for this region because of the

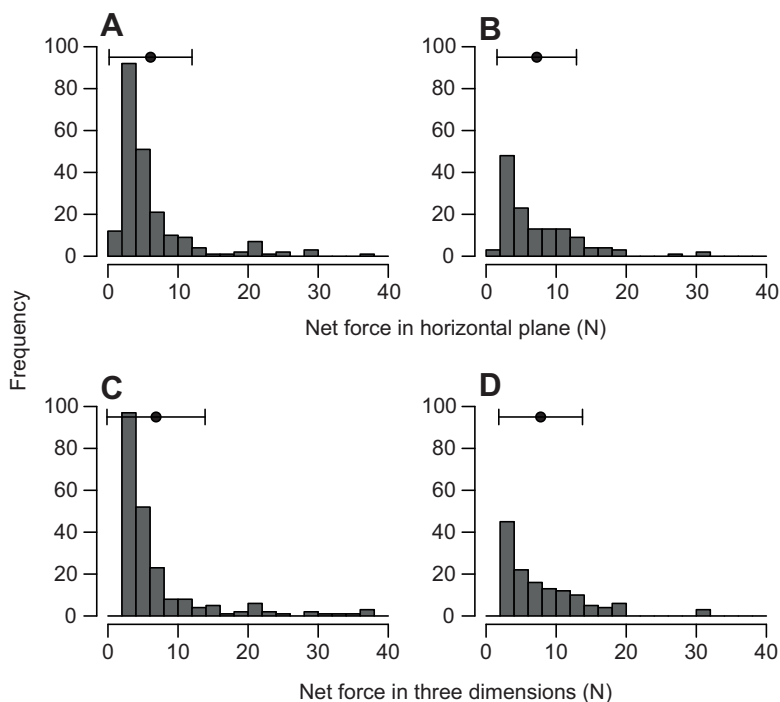
annual cycles in timing of low tide emersion (J. L. Burnaford, unpublished data). During the period of our study, the robolimpets spent more than 10 times as much time exposed to air during the hours of 08:00 to 16:00 in the winter and spring as in the summer (based on verified tidal heights from NOAA station 9410660).

### Measuring the force exerted by a black oystercatcher predator

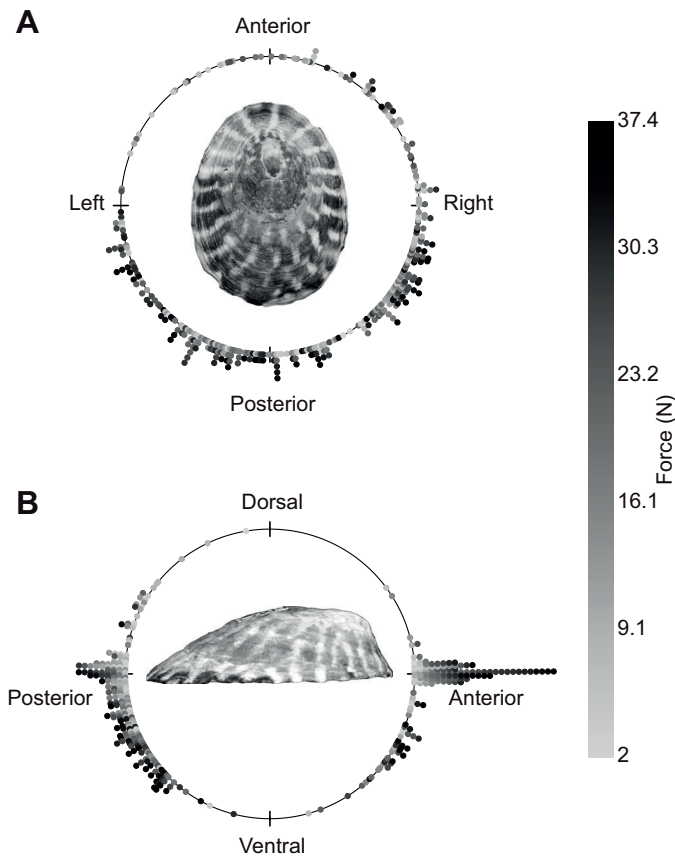
The strongest net force exerted by the captive bird on the force meter was 37.36 N, during a 'peck' event. The strongest recorded push event was 31.89 N. Pushes and pecks were both registered frequently ( $N=217$  and 136 individual events, respectively). The captive bird did frequently exert substantial force on the limpet mimic: 11.5% of 'peck' events and 13.2% of 'push' events registered as greater than 14 N (Fig. 4). Pushes lasted between 20 and 490 ms. The captive bird primarily struck at the anterior end of the shell, pushing the limpet mimic rearward (Fig. 5A). The bird tended to strike from a low enough angle to produce a force vector that was predominantly directed in the horizontal plane of the force transducer, which would create a shearing force between the limpet mimic and the substratum (Fig. 5B). The highest recorded shear force (i.e. net force recorded by the two horizontal axes of the force transducer) was 36.63 N.

### Simulated predation trials

Experimental treatment had a strong effect on the likelihood of a limpet being removed from a tile by simulated bird predation (Fisher's exact test,  $P=0.003$ ; Fig. 6). Specifically, four times as many limpets exposed to warm low tides were removed from tiles as limpets exposed to the two other treatments (which did not differ in the proportion of limpets removed; Fisher's exact test,  $P=1$ ). Yet the removal of limpets was not immediate; across all three treatments, an average of 6.36 ( $\pm 2.50$  s.d.) 14 N strikes were needed to dislodge a limpet that was eventually removed ( $N=11$  dislodged limpets). Limpets exposed to warm low tide treatments required at least five 14 N strikes for removal (mean  $\pm$  s.d. =  $7.5 \pm 1.69$  strikes,  $N=8$  limpets).



**Fig. 4. Histograms of forces exerted by the captive oystercatcher on the force transducer.** (A,B) In the horizontal plane; (C,D) in three dimensions. The left column shows events classified as pecks ( $N=217$ ), and the right column shows events classified as pushes ( $N=136$ ). Points and error bars above each histogram represent the means  $\pm$  s.d.



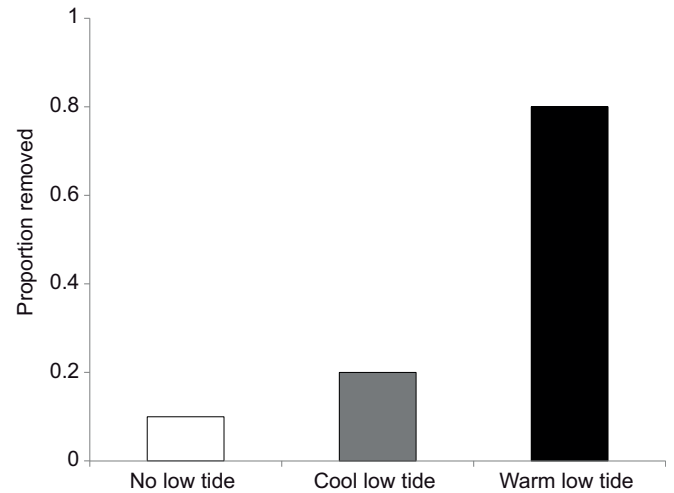
**Fig. 5. Angular distribution of force vectors for strike events along different axes of the limpet mimic.** (A) Anterior–posterior and left–right axes; (B) anterior–posterior and dorsal–ventral axes. Each point represents the resultant direction of a single strike event classified as a peck or push by the captive black oystercatcher during trials on six dates. Point colors indicate the force in Newtons in (A) the horizontal plane only and (B) the net force in three dimensions.

Simulated beak strikes frequently caused limpets to ‘slide’ on the tile even though they remained attached; only two of 30 tested limpets remained in the same location on the tile for the entire trial. However, sliding did not predict the response to subsequent strikes: limpets that ‘slid’ in response to one strike frequently remained stationary after subsequent strikes (Pound, 2017).

#### Captive bird predation trials

All 24 analyzed limpets were removed from tiles by the captive oystercatcher, and 19 were consumed ( $N=7$  of 9 WLT limpets, 6 of 7 CLT limpets, and 6 of 8 NLT limpets). The remaining five limpets were ignored by the bird after removal. Experimental treatment had no effect on whether removed limpets were consumed by the bird (Fisher’s exact test,  $P=1.0$ ).

Pre-removal bird–limpet interactions lasted from 0.07 to 21.01 s (mean $\pm$ s.d.=4.98 $\pm$ 5.61 s,  $N=24$  limpets; Fig. 7). There was no relationship between limpet size and interaction time (linear regressions with and without identified outliers, both  $F<0.99$ ,  $P>0.32$ ,  $R^2<0.05$ ). Analysis of the full data set indicated that interaction times did not differ among treatments (ANOVA on ln-transformed data:  $F_{2,21}=2.63$ ,  $P=0.095$ ). However, two data points were identified as statistical outliers using Grubbs’ test (on raw data: both  $G>2.2$ , both  $P<0.011$ ; Fig. 7). Removing outliers revealed differences in interaction times among limpet experimental treatments (ANOVA on ln-transformed data:  $F_{2,19}=3.93$ ,  $P=0.037$ ).

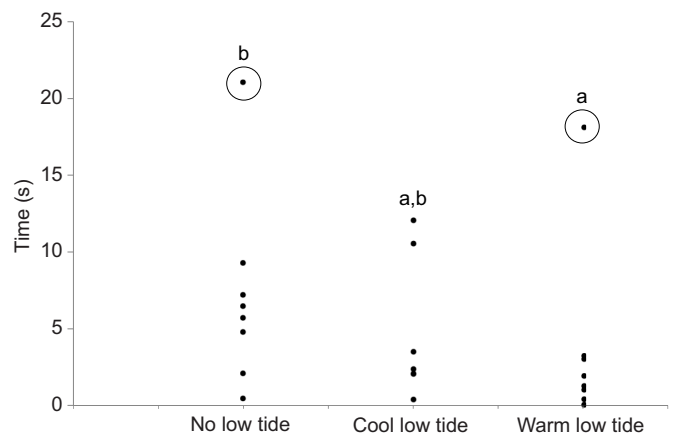


**Fig. 6. Proportion of limpets removed as a consequence of simulated bird predation in laboratory trials.** Each limpet was subjected to one 3 N strike and then to sequential 14 N strikes (to a maximum of 10).  $N=10$  limpets per treatment.

Overall, our data show a trend suggesting that individuals exposed to warm low tides were removed more quickly, on average, than limpets exposed to cool low tides or which were maintained in water (in the NLT treatment) before being exposed to the predator. The minimum interaction time before limpet removal (i.e. the fastest removal for a limpet in that treatment) was at least six times longer for limpets in CLT or NLT treatments compared with limpets in the WLT treatment. The bird removed eight of the nine limpets exposed to warm low tides in 3.25 s or less, while only four of the seven limpets exposed to cool low tides and two of the eight limpets in the no low tide treatment were removed that quickly.

#### DISCUSSION

Our data show that limpets exposed to high temperatures during low tide were removed from the substratum more quickly (simulated predation=fewer strikes, captive bird predation=less interaction time) than limpets that had experienced cooler conditions either



**Fig. 7. Pre-removal bird–limpet interaction times in captive bird predation trials.** Sample sizes are as follows:  $N=8$ , 7 and 9 limpets for the no low tide, cool low tide and warm low tide treatments, respectively. Circled points were designated as outliers using Grubbs’ test. Shared letters above treatments indicate that means are not significantly different (ln-transformed data without outliers: ANOVA  $F_{2,19}=3.93$ ,  $P=0.037$ , Tukey’s HSD  $P=0.046$ ).

during low tide or in the NLT treatment. Temperatures vary among microhabitats over space and time: on any given day at any given site, the limpet population has a patchwork of individuals with different thermal histories (present study; Denny et al., 2006). Our data suggest that this variability among individuals has important implications for species interactions, as prey thermal history directly affects tenacity, which has a direct impact on susceptibility to predation. *Lottia gigantea* resists predation by birds at low tide through a combination of muscular contractions and mucus adhesion (Fisher, 1904; Denny and Blanchette, 2000). High but sub-lethal temperatures can cause damage to or atrophy of muscular proteins (Tomanek and Zuzow, 2010; Serafini et al., 2011; Madeira et al., 2015) and can alter mucus characteristics, either of which could reduce the ability of an individual limpet to adhere to the substratum. Lifting the shell to facilitate evaporative cooling in response to high temperatures can enhance desiccation and changes in osmolarity, which could contribute to reduced tenacity (Denny and Blanchette, 2000). In addition, limpets engaged in evaporative cooling may be more susceptible to dislodgement because they are relaxed (and not holding onto the rock as tightly), because the gap between the shell and the rock surface acts as a cue for attack by foraging birds, or because the gap eliminates the contribution of the shell (working against the rock surface) to the limpet's tenacity (see Hahn and Denny, 1989). Temperature alone, or in concert with other stressors, therefore has the potential to affect resistance of *L. gigantea* to predation by oystercatchers through multiple pathways, which could have cascading effects on primary space utilization and community diversity over small and large scales in the intertidal zone owing to the important role this territorial limpet species plays in mid-intertidal zone communities.

Our work differs in several important ways from previous work on the topics of limpet adhesion and resistance to bird predation. Importantly, this study provides what to our knowledge is the first quantitative assessment of the forces exerted by a black oystercatcher during predation events on limpets. The data collected by our novel recording device allowed us to scale laboratory predation trials in terms of both applied force and number of attacks. These laboratory predation trials included a morphologically realistic beak mimic that we used to apply force at an ecologically relevant angle and location on the prey item. Our evaluation of predatory strikes by a live black oystercatcher provides important context for our understanding of the dislodgement tenacity of intertidal molluscs.

Because our captive oystercatcher was bred in captivity, our assessment of limpet resistance to predation and our measurement of maximum shear force applied during predation are unlikely to encompass all aspects of wild oystercatcher predation. Although Squeakers was developmentally and morphologically an adult at the time of this study, he was a naive limpet predator. Fledgling black oystercatchers first learn to identify limpets as prey when the parents bring food items to the nest (Webster, 1941b; Legg, 1954) and then by following their foraging parents, who turn over the limpets for their offspring to consume (Williams, 1927; Webster, 1941b). In terms of attack strategy for limpet prey, some degree of observational learning may occur as young oystercatchers follow foraging parents, although trial and error has been proposed to be the larger part of the learning process (Swennen et al., 1983). The attack behaviors Squeakers exhibited appear to be well within the range of wild oystercatcher behaviors. For example, individual *Haematopus ostralegus* attack limpet prey items using a variety of strike angles and from all directions, with most successful attacks arising from strikes on the shell anterior region (Feare, 1971;

Coleman et al., 1999; Nagarajan et al., 2015). Naive juvenile oystercatchers are commonly less efficient foragers than experienced adults (*H. ostralegus*: Goss-Custard and Le V dit Durell, 1987; *H. palliatus*: Hand et al., 2010), but this efficiency gap lasts only 3–4 months owing to the rapid learning curve for the naive birds (Goss-Custard and Le V. dit Durell, 1987). If our captive bird had not gained enough experience to reach 'wild adult' efficiency before trials began, then his predatory behavior may be closer to that of a wild juvenile. Notably, juvenile or naive birds frequently experience an 'elevated motivational state' in response to novel prey items, which results in a 'more intense' predation response relative to experienced birds (Marchetti and Price, 1989). Because limpets were novel prey, it is possible that Squeakers attacked limpets with greater force and/or greater persistence than an experienced bird, and that the forces he exerted on the force meter exceed those that would be exerted by an experienced wild forager. Alternatively, it is possible that as a naive forager, Squeakers attacked live limpets and the force meter with less force than would be exerted by a wild bird. Because wild oystercatchers avoid our force meter as they forage on rocky benches (J. L. Burnaford, personal observation), we are not yet able to put the forces measured here directly into context for wild birds. However, our data do provide a first quantitative look at the capabilities of this species.

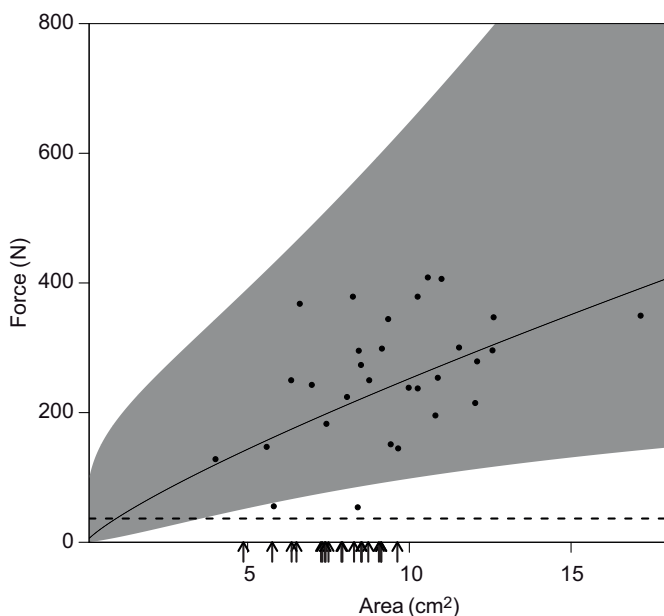
Despite the fact that our captive bird was able to remove all of the limpets in our experimental trials, we assert that differences in susceptibility to predation among treatments are ecologically significant. We presented individual limpets to a hungry predator that was enclosed with only this single food item for 30 min, 90 times longer than the maximum amount of interaction time required to remove a limpet in the warm low tide treatment. The bird frequently attacked a limpet for a short period of time, stood up and walked away, then returned to the experimental tile and attacked and removed the limpet. The maximum number of separate attacks (defined as a period with continuous strikes; if the bird stood up for 5 s or stepped away, this was considered the end of the attack) was lower for limpets in the warm low tide treatment (maximum of three separate attacks) than for limpets in cool low tide or no low tide treatments (maximum of five and nine separate attacks, respectively). In natural field conditions, with a variety of prey items available, it is far less likely that a bird that had moved away from a limpet before removing it would return to attack and remove that same limpet. A more experienced forager may have given up entirely on prey items with high tenacity rather than persisting in the attack. Similarly, in natural conditions, even a naive bird may abort an attack on a limpet with high resistance before the limpet is removed, moving on to another prey item with potentially lower resistance. Thus, our captive-bird experiments may have over-estimated the likelihood of removal for limpets in cool temperature treatments. Differences in tenacity that affect 'time to removal' could result in real differences in mortality rates under real-world conditions.

The observed attacks by the captive bird on the force transducer and live limpets would produce a combination of shearing and compressive forces on the shell. Based on the three-dimensional force transducer data, the force vector in the vertical plane was generally shallow enough – striking at an angle less than 45 deg above the horizontal – that shear forces would predominate. The shell of *L. gigantea* may be resistant enough to compressive forces that strikes normal to the plane of the substratum would fail to crack the shell, and simply result in the limpet being pushed firmly against the rock surface. It is doubtful that compressing the limpet into the rock surface would have any benefit for dislodging the animal, and



so the oystercatcher's focus on applying shearing forces would appear to be the more effective strategy. Measurements of dislodgement forces in shear and in tension (pulling the shell up from the surface) by Denny and Blanchette (2000) indicate that *L. gigantea* is more resistant to shearing forces than lift forces, but an oystercatcher is likely limited to using shearing force except in circumstances in which the beak could be inserted between the shell edge and rock surface to lift the shell. We did measure some slightly upward-directed forces on the limpet mimic, but these were rarely as forceful as the horizontal or downward-directed forces. Using data from Denny and Blanchette (2000), we estimated the 95% prediction interval for dislodgement forces applied in shear to stationary *L. gigantea* (Fig. 8). Based on their data and the 36 N maximum shear force we measured in the captive oystercatcher force transducer trials, we estimate that this oystercatcher could dislodge a strongly attached *L. gigantea* with a foot area up to 3.5 cm<sup>2</sup> with a single strike.

Tenacity is positively related to body size in *L. gigantea* (Denny and Blanchette, 2000), and individuals larger than those used in our study are commonly found in natural populations; for example, limpets longer than 40 mm made up 55% of the 31 individuals measured in long-term monitoring plots at Dana Point in autumn 2017 (Multi-Agency Rocky Intertidal Network, www.pacificrockyintertidal.org). Therefore, in natural field conditions, a large number of individuals within a population may have higher 'baseline' tenacity (before exposure to low tide conditions) than the limpets used in our study. *Haematopus bachmani* successfully attack limpets up to 80 mm in length, although individuals longer than 40 mm make up only a



**Fig. 8. Forces applied in shear required to dislodge *Lottia gigantea* of various aperture areas.** Raw data (black circles) reproduced from Denny and Blanchette (2000). The best-fit line is derived from a linear regression of the form  $\log(\text{Force}) = \log(38.66) + 0.815 \times \log(\text{Area})$ , and the 95% prediction interval is shown in gray. The dashed horizontal line indicates the magnitude of the largest shear force produced by the captive oystercatcher in the present experiment, so that regions of the prediction interval that fall below the line indicate the sizes of *L. gigantea* that might be susceptible to dislodgement by a single strike from the oystercatcher. Arrows on the horizontal axis mark the sizes of live limpets successfully removed by the captive oystercatcher in this study primarily using multiple strikes. Strike forces could not be measured for attacks on the live prey limpets.

small proportion of their diet (~10%; Legg, 1954). While successful dislodgement of large adult *L. gigantea* can be accomplished, it may require one or more of the following conditions. First, attacking limpets with repeated strikes in quick succession, a behavior observed in our captive bird trials and with wild birds (Williams, 1927; Webster, 1941a), may weaken prey items. Indeed, the live limpets dislodged by the captive oystercatcher were large enough (indicated by arrows on the horizontal axis in Fig. 8) that their tenacity may have exceeded the maximum force of a single strike, but they were often successfully removed by the bird using repeated strikes. Second, in Denny and Blanchette (2000), showed that limpet tenacity was markedly decreased when limpets were moving quickly to escape predatory seastar cues; thus, oystercatchers feeding during a falling or rising tide could seek out mobile *L. gigantea* that are taking advantage of wetted rocks to graze algae. Similarly, wild oystercatchers frequently attack limpets that are stationary but 'relaxed' (Webster, 1941a), which may be easier to remove than limpets that have been warned (e.g. by tapping on the shell as in this study and Denny and Blanchette, 2000). Third, in Denny and Blanchette (2000), measurements were made on limpets with cool body temperatures (10–15°C, Mark W. Denny, Stanford University, personal communication), so limpets experiencing higher body temperatures might become more susceptible to shear forces and therefore easier to remove, as was evident in our live limpet predation trials. If these conditions do not apply, then large limpets may experience a 'size refuge' from oystercatcher predation.

Finally, we have focused on *L. gigantea* here, but the northeast Pacific intertidal zone is home to several other smaller-bodied *Lottia* species with concomitantly lower dislodgement forces. Hahn and Denny (1989) simulated oystercatcher predation on *L. scabra* and *L. digitalis* using a transducer that was held as close to parallel to the substratum as feasible to impart a primarily shearing impact force (Mark W. Denny, Stanford University, personal communication). The dislodgement forces recorded for these smaller limpets by Hahn and Denny (1989) were in many cases lower than the maximum shear forces produced by the captive oystercatcher in this experiment, and these species often make up a substantial portion of black oystercatchers' diets (Legg, 1954; Hartwick, 1976; Frank, 1982). *Lottia scabra* situated in a deep home scar frequently had tenacities greater than an oystercatcher may be capable of producing without fracturing the limpet shell (and potentially reducing the value of the prey item for an oystercatcher), but home scars are often shallow or absent on some rock types, leaving the limpets vulnerable to oystercatcher predation (Hahn and Denny, 1989).

The difference in tenacity between heat-stressed and non-stressed *L. gigantea* shown in our simplified study strongly suggests differential attack success and mortality for prey items with different thermal histories under natural field conditions. Our conclusions should be considered conservative with respect to natural field conditions, in which foraging birds with a range of experience levels are presented with limpets of many different sizes on rugose and complex rocky surfaces, and in which the predators experience disruptive stimuli including human interference, wave action from the incoming tide, and bird competitors (Marsh, 1986; Lindberg et al., 1987; Denny and Blanchette, 2000). Our simplified predation scenario leaves several aspects of this interaction to be explored in future studies. Our set-up (unglazed clay tiles) allowed us to maintain an identical surface for limpets in all treatments, but less force was likely required to remove limpets from the smooth tiles than from natural rock substrata because substratum roughness affects tenacity in multiple animal species (Hahn and Denny, 1989;

Ditsche et al., 2014). The time between strikes in our simulated predation trials (20 to 90 s, to allow observers to assess limpet attachment and movement) was substantially longer than the time between successive strikes for our captive bird as calculated from our force meter data [Fig. 2A; median time between successive strikes in an attack (defined as a period of attack with fewer than 10 s between successive strikes) of two to 60 strikes each ranged from 0.08 to 0.39 s]. The long period between strikes in the laboratory experiment may have allowed time for recovery and led to increased limpet resistance to dislodgement relative to a predation event by a real bird. The fixed angle of attack in our simulated trials (35 deg above horizontal) was within the range used by our captive oystercatcher on the force meter (in the third quartile of downward directed strikes; Fig. 5B) and was low enough that shear forces would predominate, but our captive bird trials suggest that live birds use a variety of attack angles.

Our data highlight an important ecological consequence of spatial and temporal complexities of temperature patterns during emersion for rocky intertidal organisms both in the present climate and in the face of a warming climate. On a given day, individuals in close proximity to each other can experience very different temperatures (Denny et al., 2011), and our data provide insight into the linkages between this thermal heterogeneity and previously documented patterns of predation on limpets in intertidal systems. For example, Lindberg et al. (1998) compared *L. gigantea* distribution between vertical and horizontal surfaces at sites with and without black oystercatchers, and found that the relative distribution of limpets among rocks of different inclination matched the availability of the different surface inclinations at the sites without oystercatchers, while limpets were rarely found on horizontal surfaces at sites with oystercatchers. This pattern was attributed purely to accessibility of the prey to the predators, as limpets on vertical rock microhabitats have typically been considered to be relatively safe from black oystercatcher predation (Hahn and Denny, 1989; Lindberg et al., 1998). However, our study suggests that body temperatures, which can differ strongly among microhabitats, may be an additional factor in the spatial patterns of predation at a site. Limpets on flat rock during low tide are likely to be exposed to warmer temperatures, on average, than those located on vertical rock, and, according to our data, an oystercatcher could remove six 'warm low tide' limpets in the same amount of time as it takes to remove a single 'cool low tide' limpet (minimum time to removal 0.07 versus 0.42 s). This environmentally driven spatial and temporal variability in susceptibility to predation could be an important driver of community patterns over multiple scales.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: R.J.P., J.L.B.; Methodology: R.J.P., L.P.M., F.A.K., J.L.B.; Software: L.P.M., F.A.K.; Validation: R.J.P., L.P.M., F.A.K., J.L.B.; Formal analysis: R.J.P., L.P.M.; Investigation: R.J.P.; Resources: R.J.P., L.P.M., F.A.K., J.L.B.; Data

curation: R.J.P., L.P.M.; Writing - original draft: R.J.P., J.L.B.; Writing - review & editing: R.J.P., L.P.M., J.L.B.; Visualization: R.J.P., L.P.M., J.L.B.; Supervision: J.L.B.; Project administration: R.J.P., J.L.B.; Funding acquisition: R.J.P., J.L.B.

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#### Data availability

Data and analysis code related to this project have been archived and made publicly available at <http://doi.org/10.5281/zenodo.3731787>.

#### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.213595.supplemental>

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