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RESEARCH ARTICLE

Nest substrate and tool shape significantly affect the mechanics and energy requirements of avian eggshell puncture

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ABSTRACT

Some host species of avian obligate brood parasites reject parasitic eggs from their nest whereas others accept them, even though they recognize them as foreign. One hypothesis to explain this seemingly maladaptive behavior is that acceptors are unable to pierce and remove the parasitic eggshell. Previous studies reporting on the force and energy required to break brood parasites' eggshells were typically static tests performed against hard substrate surfaces. Here, we considered host nest as a substrate to simulate this potentially critical aspect of the natural context for egg puncture while testing the energy required to break avian eggshells. Specifically, as a proof of concept, we punctured domestic chicken eggs under a series of conditions: varying tool shape (sharp versus blunt), tool dynamics (static versus dynamic) and the presence of natural bird nests (of three host species). The results show a complex set of statistically significant interactions between tool shapes, puncture dynamics and nest substrates. Specifically, the energy required to break eggs was greater for the static tests than for the dynamic tests, but only when using a nest substrate and a blunt tool. In turn, in the static tests, the addition of a nest significantly increased energy requirements for both tool types, whereas during dynamic tests, the increase in energy associated with the nest presence was significant only when using the sharp tool. Characterizing the process of eggshell puncture in increasingly naturalistic contexts will help in understanding whether and how hosts of brood parasites evolve to reject foreign eggs.

KEY WORDS: Energetics, Egg, Peck, Puncture, Nest, Obligate brood parasite, Impact, Dynamic fracture

INTRODUCTION

Avian obligate brood parasites reduce the fitness of host species by laying their eggs in other species' nests, often damaging host eggs in the process (Hauber, 2003; Lopez et al., 2018) and altogether eliminating (Anderson et al., 2009) or taking resources away from the hosts' own young (Dearborn, 1998). Because brood parasites are detrimental to host fitness, the recognition and rejection of foreign eggs are major means of antiparasitic defense by would-be foster parents (Briskie et al., 1992; Robertson and Norman, 1976; Luro et al., 2020). Whereas the recognition of parasitic eggs is seen in a wide variety of host species, not all of these birds physically remove the foreign eggs (e.g. Antonov et al., 2008; Espinosa et al., 2012). Those that do, may eject foreign eggs by either grasping the entire egg with their beak, or by puncturing the shell with their beak to create a hole that allows them to hold the egg in a tweezer-like manner and remove it from the nest (Rasmussen et al., 2009). One hypothesis for why some hosts do not reject distinct foreign eggs is that it is too costly to do so either physically or cognitively (Manna et al., 2017). Previous studies have shown that puncture ejection is costlier than grasp ejection in terms of mistakenly damaging the host's own eggs while attempting to pierce the typically thicker-shelled parasitic egg (e.g. Rohwer et al., 1989). Here we explore the potential costs of pierce-rejecting parasitic eggs in depth by providing a proof-of-concept approach to measuring the effects of tool shape, force dynamics and nest substrate on the egg puncture process.

Egg rejection is a complex process that relies on the ability of the bird to both identify the foreign egg and then physically remove it. A great deal of work has been done both on the role of identification and cognitive processing of foreign eggs in egg rejection (e.g. Moskát et al., 2010; Spottiswoode and Stevens, 2010; de la Colina et al., 2012), and on how the shell thickness and microstructure of parasitic eggs can make it difficult to pierce and physically reject the foreign egg (Antonov et al., 2008; Igic et al., 2011; Soler et al., 2019). For example, rufous-tailed scrub robins (*Cercotrichas galactotes*) were found to identify foreign eggs in their nests at least 63% of the time, but only grasp rejected them in ∼28% of the trials (Espinosa et al., 2012). In turn, eastern olivaceous warblers (*Iduna pallida*) also clearly identified foreign eggs but were unable to reject them at all (Antonov et al., 2008). The recognition of parasitic eggs in the nest is generally considered to have taken place when the nesting birds peck at the some of the eggs to any degree (Antonov et al., 2008; Espinosa et al., 2012), because parents are not known to peck their own eggs in typical circumstances (Scharf et al., 2019). Rejection methods are also thought to be very consistent within species, with around 95% consistency of response found in blackcaps (*Sylvia atricapilla*) (Honza et al., 2007). However, the former two species seemed to have different causes for failure to reject the foreign eggs. The scrub robins were hypothesized to 'give up' based on a lack of motivation to remove the egg (Espinosa et al., 2012), whereas the warblers were physically unable to pierce the thicker parasitic eggshell (Antonov et al., 2008). Although there are many explanations as to why potential hosts may not reject parasitic eggs, it is possible that birds fail to reject owing to high mechanical and energetic costs of puncture ejection. Accordingly, multiple studies have found evidence that parasitic eggs are energetically more difficult to puncture than non-parasitic eggs (Antonov et al., 2008; Spaw and Rohwer, 1987) and, in support, the eggshells of the obligate parasitic brown-headed cowbird (*Molothrus ater*) are approximately 30% thicker than expected for their body size (Spaw and Rohwer, 1987; Lopez et al., 2018).

Here, we set out to study the dynamics of avian egg puncture in several experimental settings and contexts that have not been compared in combination previously. Much of the research done on avian egg strength has been on the shell's structure specifically and the effects of handling and processing by commercial machinery on domestic chicken (*Gallus domesticus*) eggshells (e.g. Coucke et al., 2010). Even in the

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context of avian brood parasitism, experimental studies on comparative eggshell strengths mostly pertain to laboratory settings and under slow-moving or static conditions (e.g. Polat et al., 2007; DeKetelaere et al., 2010). Such studies may not take into account several variables that could be critical to understanding the costs involved in egg puncture under more naturalistic contexts and conditions.

First, there is the morphology of the puncture tool (i.e. the beak in the case of birds). Avian beaks often covary with avian foraging ecology (Friedman et al., 2019; Pigot et al., 2020), which, in turn, covaries with egg rejection propensity across host species to avian obligate brood parasites (Luro and Hauber, 2020). Furthermore, prior research has shown that the sharpness of a puncture tool will have a large influence on how much energy is required to puncture various materials (Evans and Sanson, 1998; Freeman and Lemen, 2007; Anderson, 2018). In general, it is hypothesized that sharper tools should require less energy to puncture materials than blunter tools owing to increasing stresses at the point of contact (Anderson, 2018). Experimental studies on vertebrate teeth have supported this hypothesis (Evans and Sanson, 1998; Freeman and Lemen, 2007; Whitenack and Motta, 2010; Crofts et al., 2019). However, much of this work has been done on softer, more ductile materials (flesh and cuticle) as opposed to materials as brittle as avian eggshells, which may create different mechanical challenges (Lucas, 2004).

A second factor that has not been studied in detail is the effect of speed in eggshell puncture mechanics (Anderson et al., 2016). When a bird pecks, it is not a slow, static motion but rather a rapid, dynamic one (Scharf et al., 2019). The velocity of the pecking action combined with the mass of the bird's head will determine how much energy is applied to the eggshell. Materials often act differently when loaded under high strain rates (Anderson, 2005; Karunaratne et al., 2018) and this is particularly true of biological tissues that tend to be viscoelastic (Burstein and Frankel, 1968; Vogel, 2013). Previous experimental work on dynamic biological puncture has shown that the kinetic energy applied by the projectile is closely and positively correlated with puncture depth (Anderson et al., 2016; Anderson et al., 2019). However, these few studies focused exclusively on soft materials and as with the tool sharpness studies above, the influence of speed on fracture behavior in more brittle materials such as eggshells is unclear. The lack of detailed data on the velocity of egg pecking behavior in birds means it is unclear how much energy birds can actually apply to the shells, or how much energy is used for each individual pecking event and, cumulatively, across repeated pecks. Further, it is unknown whether applying the energy to a brittle material, such as a calcareous avian eggshell, with a higher velocity of impacts will have the same consequences as seen in softer materials (Anderson et al., 2016).

A third factor that has not been taken into account in studies of antiparasitic eggshell pecking is the effect of a soft substrate (a lined nest cup underneath the egg) on modulating the energy required to successfully puncture an egg. The parasitic egg, like the rest of the host's clutch, lays atop the nest's bottom, which is often soft and deformable compared with the hard artificial test surfaces upon which egg puncture trials are usually performed in the lab (e.g. Picman, 1997). When the puncture tool is pressed into the egg, some energy will be lost as the nest underneath compresses and deforms. A similar, measurable loss of energy owing to transfer of momentum has been illustrated in high-speed experiments on snake fangs (Anderson et al., 2019). Therefore, it is possible that the malleability of the nest substrate will cause a detectable loss of energy through deformation and require more overall energy to puncture the eggshell in this context than predicted by eggshell structure, size, thickness and microstructure alone (Soler et al., 2019).

We began our line of investigation by proof-of-concept experiments in which we sought to explore the effects of these three factors on the energy required to break a widely available avian eggshell (of the domestic chicken). To accomplish this, we performed a series of puncture experiments at both static and dynamic speeds while varying both the shape of the puncture tool (sharp versus blunt) and the substrate upon which the test was performed (hard surface versus a series of host species' nests). Our first null hypothesis was that there would be no difference in energy requirements to puncture between the tool types. Our second null hypothesis was that we would see the same effects of the 'tool type' and 'nest' variables on eggs in both speed settings. Our third null hypothesis was that there would be no difference between the different species' nests or between nest presence versus absence. Thus, we used the resulting data to test a suite of three specific alternative predictions: (1) a sharp puncture tool requires less energy than a flat puncture tool owing to the increase in stress concentration at the point of impact, (2) tool sharpness and substrate each affects puncture energy for the eggshells similarly between static and dynamic puncture tests, and (3) the eggs require more energy to be punctured when they are placed on a nest substrate because of the deflection of the softer natural substrate relative to a hard test surface.

MATERIALS AND METHODS

Materials

For all experiments, we used Dutch Farms brand Grade A Large white chicken eggs obtained from a local grocery store. The eggs had a mean±s.d. height of 56.33±1.49 mm (max.=60.60 mm, min.=52.71 mm) and a mean width at widest point of 42.97±0.68 mm (max.=44.92 mm, min.=41.25 mm). These eggs had a mean thickness of 1.31±0.04 mm (max.=1.43 mm, min.=1.19 mm). Using commercially sourced chicken eggs had the dual advantage of being fairly regular in shape and size as well as much easier to obtain in large quantities in comparison with eggs of a local, federally protected migratory North American brood parasitic species, such as the brown-headed cowbird. A total of n=160 chicken eggs were used to test the energetic consequences of varying the sharpness of the puncture tool and the substrate in both static and dynamic contexts. For each test case, we conducted 10 replicates, each with a new egg. A test case is defined by the unique combination of test speed (static or dynamic), tool shape (sharp or blunt) and substrate (one of three host cowbird species' nest or the absence of a nest).

Tool shape is represented by two extremes: blunt and sharp. To represent both shapes, we used 19.05 mm, 18 gauge stainless steel wire brads (hereafter: nails) from Hillman Fastener Corp. For the blunt surface, we used the flat head of the nail, and for the sharp surface, we used the pointed end of the same nail. Nails were purchased commercially and used as our puncture tool to minimize variation between tests and because their longer durability compared favorably to that of biological materials (actual host species' beaks) during our proof-of-concept tests. The blunt end of these nails had a diameter of 1.207 mm. The sharp end of the nails had an average sharpness index of 0.594 and an average included angle of 32.402 deg. These measurements were made according to the methods of Crofts et al. (2019). The included angle was the measurement of the angle of the tip of the object measured from 1 mm from the tip of the nail. The sharpness index (SI) was calculated using the following equation:

$$\mathrm{SI} = \frac{1}{\sqrt[3]{\left(\frac{1}{R'} + \frac{1}{R''}\right)}}, \tag{1}$$

Table 1. Dimensions of the nests used in the experiments

Species	Outside diameter (mm)	Inside diameter (mm)	Height (mm)	Cup depth (mm)	Mass (g)
NOCA	118.52	63.78	59.10	29.55	9.58
AMRO	122.33	69.51	82.39	49	256
CHSP	84.41	51.87	37.68	25	4.64

AMRO, American robin; CHSP, chipping sparrow; NOCA, northern cardinal.

where R' and R'' are the radius from the top view and side view of the nail, respectively.

To simulate how a natural egg's substrate (avian nest) affected the energy required to break the eggshell, we used empty nests of three different cowbird host species: the chipping sparrow (*Spizella passerina*), the northern cardinal (*Cardinalis cardinalis*) and the American robin (*Turdus migratorius*). The dimensions of the nests are broken down in Table 1. The material composition of the nests is also reviewed in the Discussion. These were collected as nests with cold, abandoned clutches locally in Champaign County, IL, USA, during May 2019, before the eggs hatched (so that the nest cup was still relatively deep, unlike when it has been occupied by growing nestlings) (M. E. Hauber, unpublished observations). In the figures and Results, the abbreviations for bird species were as follows: chipping sparrow, CHSP; northern cardinal, NOCA; and American robin, AMRO. Nests were collected under federal US Fish and Wildlife Service salvage permit MB08861A-1.

Static tests

To test the energy and force required to break the egg in a static setting, we used an Instron brand 5940 Single Column Tabletop Testing System (SCTTS). We set up the SCTTS so that the nail would load the eggshell until it had moved 3.5 mm downward. In addition, in all trials, we aimed to hit the widest part of the equator of the egg on each hit, which we had previously observed to be the most consistent place where rejecters aim to peck foreign eggs (Scharf et al., 2019). In all cases, the eggshell was successfully punctured within that 3.5 mm displacement. When no nest was used, we placed the egg on the hard, flat metal testing surface of the SCTTS with a single layer of paper towel to absorb spillage. We used soft clay to lightly hold the sides of the egg to prevent rolling. For the runs using real nests, the nest was placed between the egg and SCTTS testing surface and held in place by the clay.

We recorded the maximum force and the area under the force–displacement curve (work) during these experiments (Fig. 1). The area under the entire force–displacement curve was used to calculate energy used, including after the egg had begun to be punctured. This was done for two reasons. First, to be biologically relevant, the puncture would need to be deep enough for a bird to insert its beak to reject the egg. For this to happen, the puncture tool must penetrate completely through the eggshell into the interior of the egg. Second, the force used once a full puncture has been made is very close to zero and does not add considerable extra energy. This is justified because the energy recorded after puncture was almost always extremely close to zero (Fig. 1).

Dynamic tests

To test the energy and force required to break eggs in a dynamic setting, we used a pendulum built by the University of Illinois at Urbana-Champaign Life Sciences Machine Shop. The pendulum was a wooden dowel rod with a pivot point affixed to a metal stand (Fig. 2). The wooden rod weighed 62.8 g (m_{dowel}) and was 61 cm long (l_{dowel}) with an axis of rotation 15.65 cm away from the center. The bottom 3 cm of the dowel rod was cut in half to supply a flat surface on which the nail was attached using a hot glue gun. This removal of this mass was not taken into account when calculating the moment of inertia for the rod as inertia only changed by less than 5% when accounted for. The weight of the nail and glue ($m_{\mathrm{nail+glue}}$) varied from 0.10 to 0.25 g, and this was taken into account when calculating the energies required to break the egg (Eqn 2). To measure the energy required to break the egg, we lifted the bottom of the dowel rod with attached nail to known heights (h_{bottom}) at 0.3175 cm intervals and let it fall into the egg, which was located at the bottom of the pendulum's arc (Eqn 4). We again aimed to hit the widest part of the equator of the egg on each hit (see above). We repeated this, rotating the egg so that a new spot on the equator was being hit at each trial, until the egg was punctured. This was done to prevent fatigue at the point of contact from becoming a confounding factor in the experiment. It is also unlikely that birds can aim to peck the same exact spot on the egg in a natural nest with each successive peck. Preliminary observations also indicated that repeated impacts in different locations on the egg did not induce fatigue in the eggshell or decrease the energy needed to break the egg (D. L. Clark, unpublished observation). Over the course of testing, we found that replicate dynamic tests actually dulled the tip of the nail, so when testing using the sharp end of the nail, we exchanged the nail for a new one after every five tests. Although birds typically peck from above the egg (Scharf et al., 2019), a horizontal axis of impact was used here instead of a vertical impact.

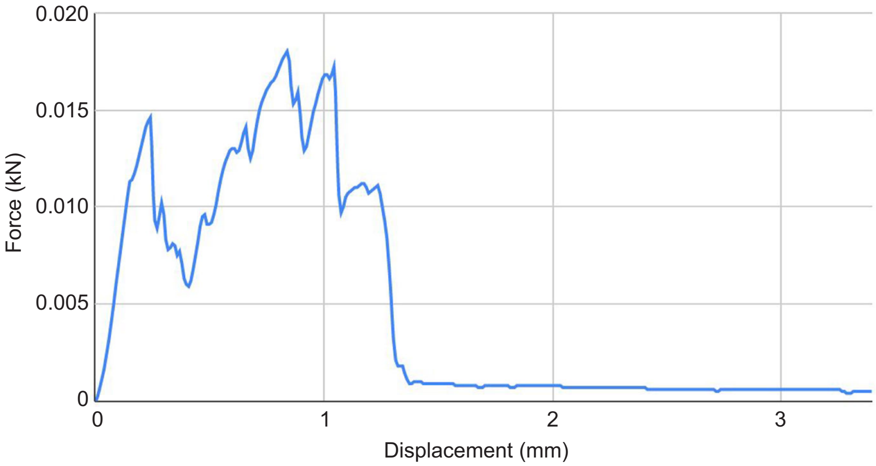

Fig. 1. An example plot taken from the Single Column Tabletop Testing System (SCTTS). The SCTTS tracked force over a displacement of 3.5 mm, which was decided based on assumptions that this distance would allow a bird to grab an egg. The energy of the puncture was calculated by taking the area under this graph. The tool had fully punctured the egg after approximately 1.3 mm of displacement, depicted by the sharp drop in force, and the force used after puncture was considered negligible.

Because of this, the nest was also held in a 90 deg shifted orientation (Fig. 3) so that the nest effects could still be detected. The decision to do this was because using a horizontal pendulum gives us more degrees to test from (180 versus 90 deg) and because a pendulum coming down on top of the egg would introduce extra force from the weight of the pendulum crashing into the egg, making it difficult to find the exact energy at which egg puncture was achieved.

We held the egg in the no-nest tests using a metal beaker holder with rubber tips in a way so that the egg would not move. When using a nest, we placed the nest in a flower pot with a piece of styrofoam supporting a cardboard platform that the nest was placed on (Fig. 3). The nest was loosely taped to the flower pot to secure it. We then placed the egg in the nest and kept it in place by taping a paper towel across the front of the egg and attaching it to both sides of the flower pot, forming a sort of 'belt', making sure that it remained low enough so that the pendulum would not hit it. The pressure introduced by the paper towel 'belt' was negligible as it was comparable to the effect of gravity in the static experiment.

To find the energy of the break point, we assumed that at the bottom of the swing, all potential energy (U) would be converted into kinetic energy (K) using the conservation of energy theorem (U=K). We therefore used the potential energy in the run where the egg broke as our measurement of energy required to break the egg. To take into account the full mass of the dowel, we utilized a series of equations to find potential energy using the height of the center of mass of the dowel. The location of the center of mass was calculated using the following formula:

$$x_{\mathrm{CM}} = \frac{m_{\mathrm{dowel}} x_{\mathrm{dowel}} + m_{\mathrm{nail+glue}} x_{\mathrm{nail+glue}}}{m_{\mathrm{dowel}} + m_{\mathrm{nail+glue}}}, \tag{2}$$

where the center of mass (x_{CM}) for the system is found using the mass (m) and center of mass (x) for the dowel, nail and glue. These values would change slightly with each nail used. The height of the drop point of the center of mass was then found using the formula:

$$h_{\mathrm{CM}} = x_{\mathrm{CM}} + \left(1 - \frac{x_{\mathrm{CM}}}{l_{\mathrm{dowel}}}\right) h_{\mathrm{bottom}}, \tag{3}$$

where the height of the center of mass relative to the table on which testing was being conducted (h_{CM}) was found using the height of the bottom of the dowel rod (h_{bottom}) and x_{CM} as known values. Finally, the potential energy was calculated using the formula:

$$U = \boldsymbol{g}(h_{\mathrm{CM}} - x_{\mathrm{CM}})(m_{\mathrm{dowel}} + m_{\mathrm{nail+glue}}). \tag{4}$$

Eqn 4 is a modified version of the potential energy formula for a stiff pendulum used to find the potential energy of the system with acceleration due to gravity ($\boldsymbol{g}$) assumed to be 9.8 m s^{-2}.

Statistical analyses

All statistical analyses were performed in R (https://www.r-project.org/). The difference in energy requirements between dynamic and static tests were first analyzed by Student's *t*-tests. Data were then broken into datasets for static and dynamic tests. An ANCOVA was run on both datasets to generate preliminary results. The formulae were aov(Energy~Nest*Tool Shape) and aov(Energy~Nest+Tool Shape) for dynamic or static tests, respectively. The data were then broken down further into subsets based on the tool used and subsets based on the nest used. Data in the tool shape subsets were analyzed using another ANCOVA with the formula aov(Energy~Nest). Data in the Nest subsets were analyzed using Welch two-sample *t*-tests. We deposited our data and R code at www.figshare.com for open access, and they are available at https://figshare.com/projects/Nest_substrate_and_tool_shape_significantly_affect_mechanics_and_energy_requirements_of_avian_eggshell_puncture/94301.

RESULTS

We found that tool shape (sharp versus blunt), the speed (stationary versus dynamic) of the impact, and a nest's presence or absence all

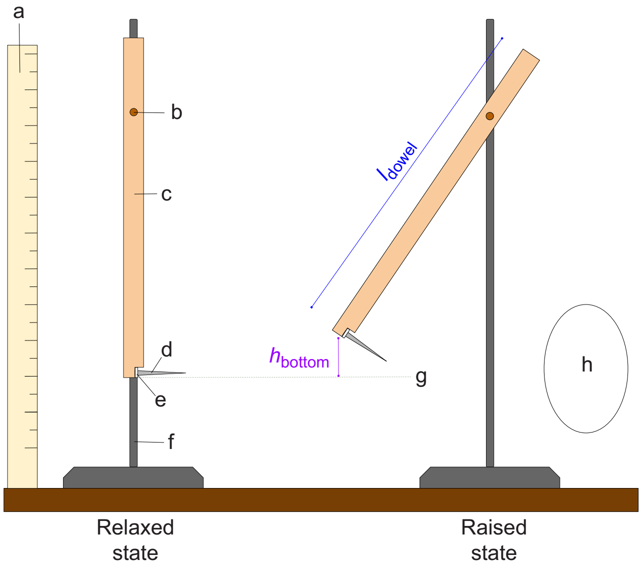

Fig. 2. Diagram of the pendulum setup used. During dynamic testing, the pendulum is lifted to a measured height as pictured in the raised stage and let go. It would swing and make contact with the egg when it entered the relaxed state. Both the weight of the nail and glue were taken into account when determining the center of mass of the pendulum system. Labeled parts of the structure are: (a) ruler used to measure the height of the pendulum before being dropped; (b) pivot point of the wooden dowel used in the pendulum; (c) wooden dowel rod, which acted as the arm of the pendulum; (d) nail used to puncture the egg; (e) cooled hot glue, used to attach the nail to the wooden dowel; (f) metal stand (the wooden dowel was attached to an arm of the stand near the top); (g) height of the bottom of the wooden dowel in its relaxed state measured on the ruler, which was used to calculate the distance between the bottom of the dowel in its relaxed state and the raised state; and (h) the egg used in the test. h_{bottom}, the height of the bottom of the pendulum in its raised state as measured by the ruler; this was used to calculate the potential energy contained in the pendulum system. l_{dowel}, the length of the dowel rod.

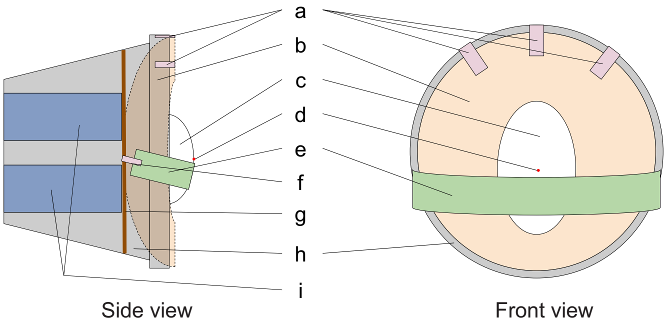

Fig. 3. Diagram of the setup used to hold the egg in place during the dynamic tests with eggs. (a) Tape holding the nest in place. (b) The nest currently being tested. (c) The chicken egg. (d) The point of contact where the tip of the nail would impact the egg surface. (e) The strap holding the egg in place. (f) The tape attaching the strap to the flowerpot. (g) A layer of cardboard which served as a backing for the nest. (h) The flowerpot that contained the entire setup. (i) Styrofoam supports to help position the nest at the correct depth in the flowerpot.

Table 2. ANOVA model run on the entire dataset in R

Stat	Sum of squares	Mean square	*P*	*F*
Dynamic				
Nest	0.00308	0.00103	**<0.0001***	8.552
Tool	0.18664	0.18664	**<0.0001***	1552.595
Nest:Tool	0.00342	0.00114	**<0.0001***	9.490
Static				
Nest	0.15516	0.05172	**<0.0001***	98.193
Tool	0.00445	0.00445	**0.00445***	8.452
Nest:Tool	0.00309	0.00103	0.11665	2.034

The values given for ‘nest’ and ‘tool’ for the static data were gathered from a model that did not use an interaction term, but the possible interaction term is included to show the lack of significance. The model run for the dynamic data did use an interaction term. Significant *P*-values are in bold and denoted with *.

had significant effects on the energy required to puncture chicken eggs. When using the ANOVA model on the data, the interaction term used in the dynamic formula was found to be significant (P<0.0001, F=9.490), while it was found to be non-significant in the static test (P=0.117, F=2.034) (Table 2).

In the static tests, a sharp tool was found to require significantly more energy to puncture the eggs than a blunt tool (P=0.004, F=8.452) (Table 2A, Fig. 4). These results, however, seemed to be entirely driven by the difference in energy requirements in the no-nest system. *Post hoc* tests showed that more energy was needed to puncture the eggshell with the sharp tool over the blunt tool only in the no-nest context (Table 4).

In the dynamic tests, the sharp tool also required significantly more energy to puncture the eggshell than the blunt tool (P<0.0001, F=1552.5) (Table 2). *Post hoc* tests confirmed that this was the case for both the nest and no-nest conditions (Table 4).

In the static system, the presence of nests significantly increased the energy required to puncture the eggs (P<0.001, F=98.193) (Table 2). *Post hoc* tests revealed that the different nests also required different energies from one another (Table 3). In the dynamic tests, the presence and type of nests also significantly raised the energy required to puncture (P<0.0001, F=8.552) (Table 2). *Post hoc* tests revealed that there was a significant difference between the no-nest condition and the robin or cardinal, but not the sparrow, nest-present conditions (Table 3).

The patterns of how the variables of tool shape, nest presence and species affected the energy required to puncture the egg were different between the static and dynamic methods of breaking eggs. Accordingly, Fig. 4 shows two starkly different patterns of data clustering that reflect these differences. In the static system, the nest presence and its type are both more important than tool shape for determining how much energy will be required to break the egg, as shown in Tables 2 and 5. Tool shape also had an effect, but only in the no-nest system (Table 4). The cardinal nests’ effect was found to be non-significant (Fig. 4). The dynamic system showed the opposite pattern, with tool shape being most important (Table 5). In the dynamic system, the presence of a nest seemed to significantly raise the energy requirements; however, the specific type of nest did not seem to significantly affect energy to puncture (Table 3). The averages for all combinations of conditions can be found in Table 6.

DISCUSSION

Static and dynamic puncture experiments on avian eggshells reveal a complex interaction between test dynamics, tool shape and substrate properties. Regarding the first hypothesis, that a sharper puncture tool would require less energy to puncture the eggshell surface, we found the opposite result from what was expected. In both static and dynamic systems, the flat nail needed significantly less energy to puncture the eggshell than the sharp one. Second, we rejected the prediction that the patterns of how the manipulated variables affected the energy required to puncture eggshells would be the same in the static versus the dynamic systems. Finally, regarding the hypothesis that eggs will require more energy to puncture when resting in a nest, we found that in both static and

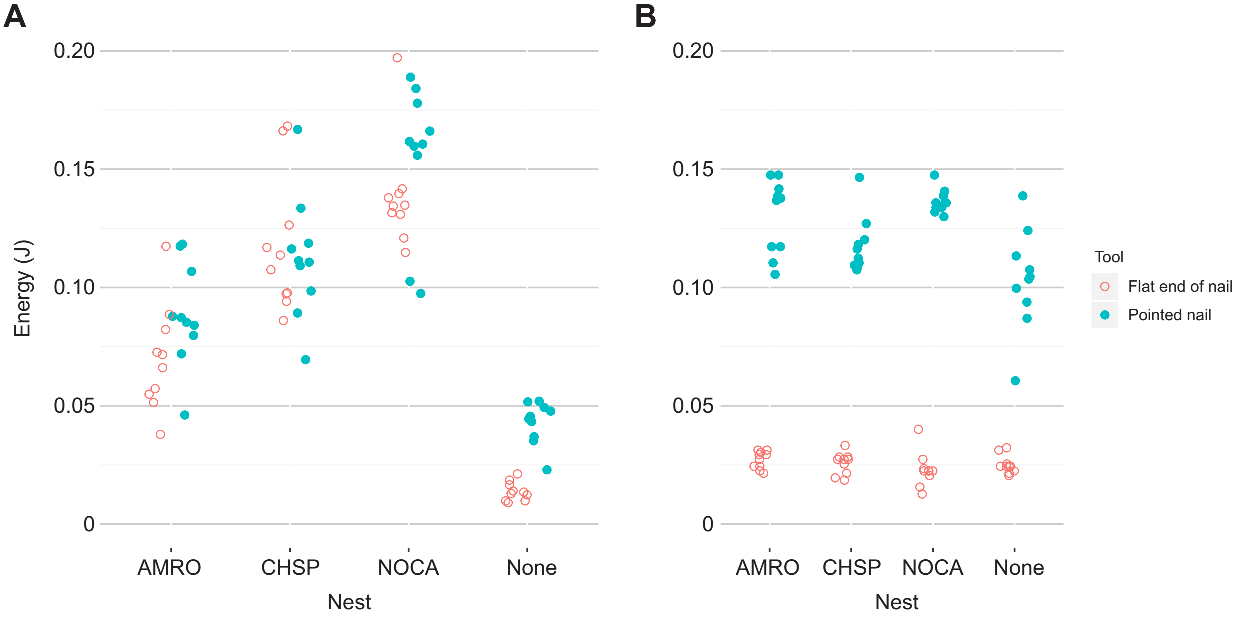

Fig. 4. Energy required to break a chicken egg in a static system and a dynamic system. The static and dynamic systems have vastly differing patterns of variable importance and energy to puncture. (A) In the static system, the type of nest seems to have the largest impact on energy to puncture, while the tool type is less consequential. (B) In the dynamic system, the tool type has a much larger impact on the energy to puncture than the nest type. More detailed statistical tests are specified in Tables 2–5 and the averages can be found in Table 6. AMRO, American robin; CHSP, chipping sparrow; NOCA, northern cardinal. A total of n=10 eggs were used for each combination of variables (tool type, nest type and speed setting).

Table 3. Tukey HSD tests between nests done with the combined tools, and separate flat and sharp tools

	Static				Dynamic			
	Difference	95% CI lower	95% CI upper	P_{adj}	Difference	95% CI lower	95% CI upper	P_{adj}
Combined tools								
CHSP–AMRO	0.0356545	0.01658487	0.05472413	**<0.0001***	−0.0069375	−0.016056256	0.002181256	0.1972327
NOCA–AMRO	0.067704	0.04863437	0.08677363	**<0.0001***	0.001074	−0.008044756	0.010192756	0.9896083
None–AMRO	−0.0509	−0.06996963	−0.03183037	**<0.0001***	−0.0144115	−0.023530256	−0.005292744	**0.0005009***
NOCA–CHSP	0.0320495	0.01297987	0.05111913	**0.000192***	0.0080115	−0.001107256	0.017130256	0.1050873
None–CHSP	−0.0865545	−0.10562413	−0.06748487	**<0.0001***	−0.007474	−0.016592756	0.001644756	0.1457037
None–NOCA	−0.118604	−0.13767363	−0.09953437	**<0.0001***	−0.0154855	−0.024604256	−0.006366744	**0.0001669***
Flat tool								
CHSP–AMRO	0.047408	0.021542199	0.0732738	**0.0001039***	−0.001466	−0.007544182	0.004612182	0.9150068
NOCA–AMRO	0.068382	0.042516199	0.0942478	**<0.0001***	−0.004201	−0.010279182	0.001877182	0.2624218
None–AMRO	−0.056226	−0.082091801	−0.0303602	**<0.0001***	−0.002051	−0.008129182	0.004027182	0.8002685
NOCA–CHSP	0.020974	−0.004891801	0.0468398	0.1471208	−0.002735	−0.008813182	0.003343182	0.6234871
None–CHSP	−0.103634	−0.129499801	−0.0777682	**<0.0001***	−0.000585	−0.006663182	0.005493182	0.9937864
None–NOCA	−0.124608	−0.150473801	−0.0987422	**<0.0001***	0.00215	−0.003928182	0.008228182	0.7767453
Sharp tool								
CHSP–AMRO	0.023901	−0.004355571	0.05215757	0.1222303	−0.012409	−0.030067731	0.005249731	0.2491566
NOCA–AMRO	0.067026	0.038769429	0.09528257	**<0.0001***	0.006349	−0.011309731	0.024007731	0.7681211
None–AMRO	−0.045574	−0.073830571	−0.01731743	**<0.001***	−0.026772	−0.044430731	−0.009113269	**0.001297***
NOCA–CHSP	0.043125	0.014868429	0.07138157	**0.0011992***	0.018758	0.001099269	0.036416731	0.0337584
None–CHSP	−0.069475	−0.097731571	−0.04121843	**<0.0001***	−0.014363	−0.032021731	0.003295731	0.1452277
None–NOCA	−0.1126	−0.140856571	−0.08434343	**<0.0001***	−0.033121	−0.050779731	−0.015462269	**<0.0001***

Significant differences are in bold and noted with *. The tests were separated into those done under static and dynamic conditions. The analysis was then broken down further into only those done with the flat tool and only those done with the sharp tool.

dynamic systems, the presence of a nest significantly increased the energy requirement to puncture the eggshell.

Regarding the effects of tool shape, it is perhaps surprising that in both the static and dynamic tests a blunt tool would require less energy to puncture than a sharp one (Fig. 4, Table 2). While this result runs counter to most previous puncture work done on biological tissues (Evans and Sanson, 1998; Freeman and Lemen, 2007; Whitenack and Motta, 2010; Crofts et al., 2019), those previous studies were focused on softer, more ductile materials such as meat or cuticle. For brittle materials, such as calcite-based eggshells, it has been suggested that a blunt tool would be more efficient in causing fracture (Lucas, 2004). Evidence for this has been shown in work on blunt dentitions in vertebrates (Berthaume et al., 2010; Crofts, 2015; Kolmann et al., 2015). Our results seem to lend further experimental support to this idea. Critically, the results relating to tool shape also have implications for egg rejection in nature. Accordingly, the beak shape of a host species may have a large effect on that bird's ability to pierce a parasitic eggshell: we predict that birds with sharper beaks would need to input more energy into puncturing a parasitic eggshell before tweezing, lifting and rejecting it.

Our second finding is that the speed of impact in a puncture situation not only dictates how much energy is provided, it also changes how other variables impact the system's output (i.e. energy required to pierce the eggshell). In a static setting, the nest presence was the most important variable tested (see below), whereas in a dynamic setting the tool type was the most important variable. These results can be viewed in light of what is known about strain rate effects on materials. Most materials become more resistant to deformation when loaded at higher strain rates (Anderson, 2005; Karunaratne et al., 2018). Recent work on ballistics gelatin showed that the volume of material deformed during high-speed (14–$20\ \mathrm{m\ s^{-1}}$) impact was inversely proportional to the speed of the impact (Anderson et al., 2016). The increased speed in the pendulum experiments may mean that the nests are less able to deform and, therefore, have less influence on the energy required for puncture than tool shape (although they still have a statistically detectable effect; see below). There is a lack of quantitative data for strain rate effects on biological tissues outside of what has been done on mammalian soft tissue for biomedical studies (McElhaney, 1966; Van Sligtenhorst et al., 2006; Pervin and Chen, 2009; Nie et al., 2011; Comley and Fleck, 2012; Farid et al., 2017). One study found that velocity had a significant effect on the brittle material polymethyl methacrylate (PMMA) (Segreti et al., 2004), but this material is very different than eggshells, and neither PMMA nor

Table 4. *Post hoc* Welch's two-sample *t*-test run on the differences in energy required to break between tool types for tests done in the dynamic and static systems

Nest	*P*	*t*	d.f.	Mean flat group	Mean sharp group	95% CI low	95% CI high
Dynamic							
None	**<0.0001***	−11.53	9.5915	0.02511	0.103269	−0.09335	−0.06297
AMRO	**<0.0001***	−20.073	9.9744	0.027161	0.130041	−0.1143	−0.09146
CHSP	**<0.0001***	−22.88	11.577	0.025695	0.117632	−0.100728	−0.08315
NOCA	**<0.0001***	−40.622	15.914	0.02296	0.13639	−0.1194	−0.1075
Static							
None	**<0.0001***	−9.3822	12.419	0.013772	0.042896	−0.03586	−0.02239
AMRO	0.07782	−1.8702	17.981	−0.069998	0.08847	−0.03922	0.00228
CHSP	0.6861	0.41081	17.802	0.117406	0.112371	−0.02074	0.03081
NOCA	0.1772	−1.4106	16.253	0.13838	0.155496	−0.04281	0.008573

Significant values are in bold and noted with *.

Table 5. ANOVA model run on the dataset excepting the no-nest system in R

Predictor	d.f.	Sum of squares	Mean square	*P*	*F*
Dynamic					
Nest	2	0.00076	0.00038	**0.01532***	4.519
Tool	1	0.15836	0.15836	**<0.0001***	1892.288
Nest:Tool	2	0.00116	0.00058	**0.00214***	6.901
Static					
Nest	2	0.04588	0.022941	**<0.0001***	34.450
Tool	1	0.00156	0.001556	0.132	2.336
Nest:Tool	2	0.00174	0.000871	0.275	1.323

The values given for 'nest' and 'tool' for the static data were gathered from a model that did not use an interaction term, but the possible interaction term is included to show the lack of significance. The model run for the dynamic data did use an interaction term. Significant *P*-values are in bold and noted with *.

mammalian soft tissue is expected to be similar to the properties of bird eggshells. More work on strain rate effects in brittle biological structures is needed to fully understand the results seen here. What our results do imply is that the speed of impact of a bird's beak on an egg during pecking will potentially influence the energy required to puncture the egg.

Our third finding is that the presence of a nest significantly raises the energy requirements for egg puncture in both the static and dynamic settings (Table 2) (the one exception being when using a blunt tool in the dynamic system). This has important methodological implications when evaluating an eggshell's resistance to piercing. Prior puncture tests done without a nest or nest equivalent may have been underestimating the energy required to puncture the eggshell in an ecologically relevant setting. While this may not be of relevance to research on eggshell strength in the food sciences or commercial fields, it will have strong relevance for behavioral ecologists interested in understanding antiparasitic egg piercing dynamics by hosts in a natural setting. The type of nest was found to have a significant effect on energy requirements to a greater or lesser extent in either the static or the dynamic tests, respectively (Fig. 4, Table 5). This implies that when conducting tests across multiple host species, the nest structure associated with the host species' identity is also important to take into account. Even though the extent of the impact of this pattern was reduced in the dynamic system, it was still statistically significant, indicating that measures should be taken to replicate accurate contexts of different species nests in the more realistic dynamic tests as well, to best replicate natural scenarios in the wild. The composition and size of different bird species nests are what gives them their unique properties. For example, our examples of chipping sparrow (smallest) and northern cardinal (intermediate size) nests were mostly composed of small sticks, strings and feathers, and lined with grass and leaves. In turn, American robin nests (largest) were also composed of a dried mud cup base underneath the plant material lining of the nest. The effects of these different sizes and compositions may account for the nest-substrate-dependent differences seen in the different tests' energy requirements (Fig. 4).

Table 6. Average energy required to puncture the eggshell for all combinations of treatments

Mode	Tool	Nest	Energy to puncture (J) Mean	s.d.
Dynamic	Flat end of nail	AMRO	0.055274	0.0074857660
		CHSP	0.052781	0.0093206920
		NOCA	0.046724	0.0148272596
		None	0.021132	0.0007495599
Dynamic	Pointed nail	AMRO	0.26877	0.0327059183
		CHSP	0.241055	0.0241275703
		NOCA	0.277556	0.0100114559
		None	0.051657	0.0078735691
Static	Flat end of nail	AMRO	0.069998	0.0224436657
		CHSP	0.117406	0.0288157053
		NOCA	0.13838	0.0222440404
		None	0.013772	0.0039853225
Static	Pointed nail	AMRO	0.08847	0.0217207044
		CHSP	0.112371	0.0259194446
		NOCA	0.155496	0.0312640039
		None	0.042896	0.0089708964

One ecological aspect of the nest structure that was not taken into account here is the potential presence of other host eggs in the nest (e.g. Lopez et al., 2018). Generally, brood parasites lay eggs in nests where there are already (some) host (and parasite) eggs in the clutch (Geltsch et al., 2016). The presence of other similarly brittle objects may reduce the damping effect of the softer nest substrate seen in our experiments. Furthermore, the presence of host eggs may also introduce another potential cost to the host, namely, the accidental breakage of their own eggs either by inaccurate pecks or by the transfer of energy between foreign and host eggs during pecking (Peer et al., 2018). Future work could address this by examining the physical effects of having multiple eggs in a nest during egg piercing attempts (Lopez et al., 2018) to generate ecologically relevant contexts when considering egg puncture.

The chicken eggs in our study were much larger and harder relative to cowbird eggs as well as to most other bird eggs that would be studied in the context of brood parasitism (Hauber, 2014). Indeed, chicken eggs require much more energy to break relative to cowbird eggs (D. L. Clark, unpublished data). However, our experiment was meant to serve as a proof of concept and to test three of the many variables contributing to egg puncture events. The focus was not on the absolute energy of the egg puncture event, but rather the relationship between the energy required to puncture and our three focal variables. We also observed that bird beaks vary in sharpness and ranged from around as sharp to much sharper than the nails used in the experiment (D. L. Clark, unpublished data). In contrast, the blunt end of the nail does not correspond to any real-world avian beak, but rather was used as an extreme that might represent fully dulled beaks.

Another set of observations made during testing was the dulling of the sharp end of the nails over a repeated number of uses when initially conducting dynamic tests. We made sure this would not affect the experiment by regularly switching out nails. However, it is worth pointing out that if repeated impacts on an avian egg can dull a metal nail, then it is feasible to consider that repeated ejection attempts could also damage a bird's beak in nature, suggesting an additional, previously unconsidered cost to antiparasitic egg rejection behaviors. Accordingly, previous research has also shown similarities in stress–strain curves between avian beak keratin and steel nails (Meneghetti, 2007).

The outputs of our experimental systems generated here could help us understand why some bird species may not reject brood parasitic eggs. The data support the prediction that birds with sharper beaks will have increased energy requirements to eject an egg from their nest through puncture rejection. Many of the hosts of brood parasitic brown-headed cowbirds, for example, do not have the beak size (length) necessary to grasp eject eggs, and so must rely on puncture ejection, if at all possible (Rohwer and Spaw, 1988). However, the increased energy requirement required when having a sharper beak may result in increased beak damage to birds with such beaks. It has been found that wear and tear on animals' biological 'tools' can have costs to the animals themselves (Persyn et al., 2004). This means that the beak damage, even if small, could affect the birds' foraging abilities, likely decreasing their survival and overall fitness. Accordingly, in a recent comparative study, the foraging ecology (which is known to shape beak morphology; Pigot et al., 2020) of hosts of brood parasitic birds was found to covary with patterns of egg rejection (Luro and Hauber, 2020). Beak morphology also affects birds' abilities to preen their feathers and remove ectoparasites (Clayton et al., 2005), which could also result in reduced fitness following beak damage. Finally, previous experiments on cowbird eggshell puncture energies were not conducted on eggs in nests (e.g. Picman, 1989), meaning that the energy requirements predicted by these prior studies may likely remain underestimations. Future work on piercing of actual cowbird and other brood parasitic eggshells should take this important methodological factor into account when designing and conducting new experiments.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: D.L.C., M.E.H., P.S.L.A.; Methodology: D.L.C., M.E.H., P.S.L.A.; Validation: M.E.H., P.S.L.A.; Formal analysis: D.L.C., M.E.H., P.S.L.A.; Investigation: D.L.C.; Resources: D.L.C., M.E.H., P.S.L.A.; Data curation: D.L.C.; Writing - original draft: D.L.C.; Writing - review & editing: M.E.H., P.S.L.A.; Visualization: D.L.C.; Supervision: M.E.H., P.S.L.A.; Project administration: M.E.H., P.S.L.A.; Funding acquisition: M.E.H., P.S.L.A.

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Data availability

Data and R code are available from figshare: https://figshare.com/projects/Nest_substrate_and_tool_shape_significantly_affect_mechanics_and_energy_requirements_of_avian_eggshell_puncture/94301.

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