1. INTRODUCTION
Many animals behave like architects [1–3], moulding their surrounding physical environments to create homes and other constructs, which serve vital reproductive and survival functions. Examples of animal architecture include the giant mounds erected by termite colonies, the casings constructed by caddis fly larvae, the elaborate nests woven by weaver birds and the lodges built by beavers, all of which provide protective barriers and safe havens within which the builders live [1]. Remarkably, many animal architectural creations rival those of humans in the perfection and scale of their design [3], and it is thought that these creations function as a sort of ‘extended phenotype’ [4], their designs being optimized by natural selection on the architects’ genes.

In contrast to animal architects, other animals are more opportunistic, moving into discarded dwellings or remnant residences that they did not themselves build [5]. A well-known example of such opportunism is that of hermit crabs [6], most species of which must protect their vulnerable abdomen [7] by occupying empty gastropod shells—what Karl von Frisch called ‘ready-made accommodation’ [1, p. 21]. Recent evidence, however, has suggested that certain hermit crabs may be more than mere occupants. While no hermit crabs have been found to build their own homes, terrestrial hermit crabs (Coenobita spp.)—but not marine hermit crabs—have been found to act as secondary architects, remodelling the interiors of the shells they inherit from gastropods [8]. In the first study of shells from before-to-after they were remodelled, the remodelled shells were found to be nearly twice as spacious as the original unremodelled versions [8], a change of potential evolutionary value to the crabs, given their continual pursuit of larger homes [6]. Critically though, the crabs generated this extra space within their homes by eliminating much of the shell’s interior (including the entire core structural support provided by the columella) and by thinning the walls at the outer lip of the aperture by more than half their original thickness [8].

Such home remodelling—in particular, the reduction of the relative barrier between the occupant and the outside world—could incur a potential cost to crabs, because less fortified homes may be more easily damaged [9], particularly by predators. Predation forces can be strong on hermit crabs [10]. In the population where remodelling was demonstrated [8], hermit crabs are sometimes subject to attack by mammals, such as raccoons, coatis or possums, which can crush shells in their mouths to access the crabs inside: smashed shell fragments and associated crab body parts (see the electronic supplementary material, figure S1) can be found where these mammalian predators have recently foraged; so predation may exert an important selective pressure upon the crabs.

No study, however, has investigated whether the remodelling behaviour of secondary architects, such as hermit crabs, might increase the cost of predation by generating homes that can be more readily crushed by predators. Here we provide the first investigation of the crushability of unremodelled and remodelled homes, subjecting them to standardized crush tests in the laboratory. We show that remodelled homes are significantly less resistant to being crushed and may thus represent a heightened danger for crabs inside.

*Author for correspondence (mlaidre@berkeley.edu).
2. MATERIAL AND METHODS

2.1. Shell acquisition

Shells were acquired during a large-scale field experiment in which over a thousand empty gastropod shells (Nerita scabricosta) were introduced to a population of terrestrial hermit crabs (Coenobita compressus) in Costa Rica (see [8] for details). The present study used three categories of shells from the experiment, referred to interchangeably as ‘homes’: new, recovered and natural homes (exemplar pictures in Laidre [8, fig. 1]). New homes were unremodelled: the gastropod body had been removed from these shells, but the shells had never been occupied by hermit crabs. Recovered homes were originally introduced to the hermit crab population as new shells; they were subsequently recovered 1 year later, at which point they had all been remodelled by the hermit crabs. Natural homes were present in the hermit crab population before the experiment; every natural shell that has been checked in this population has always been in a remodelled state.

On the basis of these three categories, triplets of shells (one new, one recovered and one natural) were chosen such that all three fell within 1 mm in diameter from one another. A total of 45 shells were tested (see below), encompassing 15 matched triplets. No significant difference existed in diameter across the three categories (one-way ANOVA: \( F_{2,42} = 0.03, p = 0.98 \); mean diameter in mm ± s.e. for new: 26.39 ± 0.86; recovered: 26.14 ± 0.77; and natural: 26.23 ± 0.78).

2.2. Shell crushing

We used an Instron 8871 universal testing machine (Instron Corporation, Canton, MA, USA) to determine each shell’s maximum compressive load—the ultimate force that the shell could tolerate before fracturing. The machine is powered by a servohydraulic actuator that can generate a maximum force of 10 kN. It is fitted with a load cell that can measure a maximum force of 5 kN, with a resolution of 0.00001 kN.

Shell specimens were tested individually by placing them inside the machine between the flat portions of two steel cylinders (compression platens), each measuring 5 cm in diameter. First, each shell was put in the same standardized position, with its aperture facing down, touching the flat portion of the bottom platen. In this position, the shells were maximally stable for crushing. The upper platen was then manually moved down until it contacted the top of the shell (figure 1a). Next, the upper platen was lowered another 2 mm under computer control, at a rate of 5 mm min⁻¹. In all cases, this descent caused a fracture of the shell within seconds (figure 1b and electronic supplementary material, figure S2). Surrounding plastic contained the shell fragments that flew out during crushing. Experiments were conducted at room temperature—close to temperatures in the field—and in air, the primary atmosphere occupied by terrestrial hermit crabs, including when they are predated. No animals were harmed because all hermit crab occupants were removed from the shells beforehand.

3. RESULTS

There was a significant difference in the maximum load that could be tolerated across the three home categories (one-way ANOVA: \( F_{2,42} = 33.71, p < 0.0001 \); figure 2). New homes tolerated significantly more load when compared with recovered homes (contrast test: \( F_{1,42} = 43.85, p < 0.0001 \)) and compared with natural homes (contrast test: \( F_{1,42} = 56.47, p < 0.0001 \)). Indeed, on average, new homes were two to three times as strong as recovered and natural homes. There was no difference, however, between the load tolerated by recovered versus natural homes (contrast test: \( F_{1,42} = 0.80, p = 0.38 \)). The fragments produced by the machine after crushing a home (figure 1c) were similar to those found in the field following predation (see the electronic supplementary material, figure S1). In all cases, the shells fractured with a clean break that extended along their length and thus would have provided ready access for a predator to any hermit crab inside.

4. DISCUSSION

Remodelled homes were far more easily crushed than unremodelled homes. Hermit crabs therefore appear to increase their susceptibility to predation by remodelling their homes. Yet, animal architects are predicted to craft architectural productions to an optimal design, one that maximizes their contribution of genes to future generations [1–4]. Why then would the crabs, as secondary architects, engage in remodelling if it increases their risk of being predated? The answer may involve a combination of (i) benefits of remodelling (which may outweigh its costs); (ii) constraints (which prevent crabs from acquiring more spacious homes by means other than remodelling); and (iii) performing remodelling only up to certain thresholds, so that alternative prey items remain more attractive to predators.

Remodelling can yield benefits to crabs, generating homes with nearly double the internal volume [8], thereby allowing females to brood more eggs and males to grow larger, both of which enhance reproductive success [6]. Additionally, remodelling produces lighter homes that are approximately two-thirds the home’s original weight [8], which can save crabs energy while carrying their home [11], especially given the variable travel distances of their scavenging lifestyle [12,13]. Besides these benefits of remodelling, crabs may also be constrained in their opportunities for acquiring spacious, lightweight homes via alternative means. Hermit crabs in general [6], and terrestrial ones in particular, are highly shell limited [14], so few opportunities may arise during a crab’s lifetime to move into a shell superior to its current one. Indeed, acquiring a superior shell may necessitate physical fights to remove a con-specific from its shell [15], which, in marine hermit crabs, can require large energy reserves and physiological costs. Thus, remodelling one’s current shell may be a better alternative.

Even after a shell is remodelled, the altered predation risk may be tolerable to hermit crabs if other, sympatric prey provide more desirable targets for predators. For instance, brachyuran land crabs, which do not occupy
gastropod shells, might possess carapaces that are more breakable than even the remodelled homes of hermit crabs (M. E. Laidre 2012, personal observation, of predated *Gecarcinus quadratus* specimens). Thus, although remodelled homes have reduced thickness and structural support compared with unremodelled homes, they could remain more formidable barriers than the exoskeletons of other crab species, and this possibility should be investigated. Interestingly, predators such as raccoons (*Procyon* spp.) can exert maximum bite forces on the order of 0.346 kN [16], a value far below that required in the present study to crush unremodelled homes, but close to that required to crush remodelled homes (figure 2). The threshold to which crabs remodel their homes might thus be set by the bite force of predators, with crabs that remodel too much being culled from the population. Of course, the cusps on predators’ teeth could provide more exacting pressure points for crushing, but we expect that the stark differences we found in our controlled laboratory tests between remodelled and unremodelled homes likewise apply in nature.

Broadly, the act of remodelling suggests that an architectural achievement’s original design has become less than optimal for its current function [1]. Home remodelling by terrestrial hermit crabs makes sense in this light,

![Figure 1](http://rsif.royalsocietypublishing.org/)

**Figure 1.** (a) Before and (b) after home was crushed in machine, with (c) resulting fragments. (Online version in colour.)

![Figure 2](http://rsif.royalsocietypublishing.org/)

**Figure 2.** Force (mean ± s.e.) to crush new, recovered and natural homes. New homes were unremodelled, while recovered and natural homes were remodelled (see text). Red dashed line denotes maximum bite force of raccoons, *Procyon* spp. (Online version in colour.)
given the dramatic differences between the marine environment (inhabited by the original shell builders, the gastropods) and the terrestrial environment (inhabited by the subsequent shell occupants, the hermit crabs): optimal shell architecture probably differs between these two habitats [9]. Even within a single habitat though complex trade-offs influence what constitutes an optimal home for hermit crabs [10], involving a variety of costs, benefits, constraints and alternatives. A complete picture of optimality can emerge only when all these variables are accounted for. The current study contributes to this holistic picture by revealing that home remodelling, while beneficial to hermit crabs in some ways, is not without potential costs. Future studies investigating the mechanisms underlying home remodelling, which remain to be elucidated, may reveal additional costs, such as the time and energy needed to re-sculpt a shell’s interior.

We thank Tom Libby, Bob Full and Mimi Koehl for discussion prior to experimentation. Supported by a Miller Institute fellowship to M.E.L.

REFERENCES