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When to socialize: perception of time-sensitive social structures among social hermit crabs

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Animals have been specialized by natural selection to perceive features of their environment that strongly impact their reproductive success. For many social animals, the social world of conspecifics provides the most pertinent information, ultimately enabling individuals to adaptively anticipate future events, like time-sensitive opportunities to acquire rare resources. Here we investigated whether 'social timing'—joining others at the right time for resource acquisition—ultimately drives the perception of different social structures among highly social terrestrial hermit crabs, *Coenobita compressus*. These crabs are specialized to live in architecturally remodelled homes, which can only be acquired through coordinated social interactions among conspecifics. We experimentally simulated these social interactions using static arrays of shells that mimicked the temporary social structures formed at each stage in the social shell-acquisition process. Free-wandering crabs in the wild were then allowed to choose among these different social structures. We found that crabs were most attracted to social structures representing early stages of the social shell-acquisition process, which predict forthcoming opportunities and hence allow individuals to join in time to take priority spots in ensuing social formations. In contrast, social structures representing late stages of the social shell-acquisition process were less attractive. When crabs joined such late-stage social structures they did not stay long, assessing they had arrived too late to insert themselves into the existing social arrangement. Broadly, these results suggest that strong selective pressures exist for sensory specializations that are in tune with the temporal and spatial patterning of opportunities in the social world.

Animals acquire and use information about their environments, which enables them to reduce uncertainty and make informed decisions, ultimately enhancing their reproductive success (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). At a proximate level, information can be gleaned from both abiotic and biotic sources using a wide range of sensory modalities (e.g. visual, acoustic, vibratory, chemical and tactile; Stevens, 2013). By gathering information from multiple independent sources, animals can potentially increase certainty about key variables (Laidre, Lamb, Shultz, & Olsen, 2013). For highly social animals, one of the most salient sources of information derives from the social environment, as represented by conspecifics and their social cues and signals (Bonnie & Earley, 2007; Danchin, Giraldeau, Valone, & Wagner, 2004; Rieucau & Giraldeau, 2011). By attending closely to conspecific behaviour and specializing on socially acquired information, many animals are able to make more informed decisions spanning an array of contexts, from foraging and fighting to mate choice to antipredator behaviour (Arnott & Elwood, 2008; Valone, 2007).

Across the diverse contexts in which animals gather information, it is often essential for them not only to read the current state but also to predict events that may unfold in the future (Laidre, 2005, 2009). Indeed, when time is of the essence, the ability to anticipate what will happen next can be vital to survival and reproductive success: it allows animals to strategically distribute themselves in space and time in advance (e.g. arriving at forthcoming opportunities ahead of competitors, rather than after it is too late and the resource is gone). Particularly in fission–fusion populations (Couzin & Laidre, 2009), in which individuals move opportunistically between fluid subgroupings based on resource availability, individuals must constantly assess whether they will be at the right place at the right time when limiting resources become available. Strategic timing and predicting future events being key, it can pay animals to be highly attuned to the social world: the momentary behaviour of conspecifics often provides a window into events to come (Seppänen, Forsman, Mönkkönen, & Thomson,

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2007). For example, the prospect of mating opportunities on the horizon can be predicted by simple social cues regarding the relative spatial positioning of key players (Crockford, Wittig, Seyfarth, & Cheney, 2007). More generally, for animals to adaptively anticipate urgent events in which timing is of the utmost importance, social information may prove indispensable.

In terrestrial hermit crabs (*Coenobita* spp.), strategic timing and reliance on social information are crucial for the acquisition of these animals' most important resources: shells. Unlike marine hermit crabs (Hazlett, 1981; Laidre & Trinh, 2014), which can simply live in any shells derived from gastropods (Alcaraz & Jofre, 2017; Laidre, 2011), terrestrial hermit crabs are specialized to live exclusively in remodelled homes—shells which were architecturally modified by earlier generations and are then reused by many future generations (Laidre, in press; Laidre, Patten, & Pruitt, 2012; Laidre & Vermeij, 2012). After an early life stage, terrestrial hermit crabs cannot remodel shells themselves (Laidre, 2012a), so they can only move up in the housing market and acquire bigger homes through coordinated social interactions with conspecifics. These social interactions entail one crab forcibly evicting another (Osorno, Fernández-Casillas, & Rodríguez-Juárez, 1998), while other congregated crabs immediately move into the shells left behind once the evictor and a series of other participating crabs have swapped (Laidre, 2014). Critically, this social shell-acquisition process and its so-called 'vacancy chains' (Chase, 2012; Chase, Weissburg, & Dewitt, 1988; Laidre, 2012b; Lewis & Rotjan, 2009) involve several key steps for terrestrial hermit crabs, in which interacting individuals form temporary, stereotypical social structures (Fig. 1). This social process begins when individuals congregate at unusually high densities (≥3 in a small area; Laidre, 2010). Next, the individuals in this group come into tactile contact, assessing for weakness that will enable one individual to evict another. Finally, as an evictor begins pulling another individual out of its shell, the rest of the individuals line up in a size-ordered chain. Each individual in the chain piggybacks on the shell of a larger crab ahead of it in line, so that once a vacancy is catalysed, all can swap in rapid succession into the next larger shell up. Notably, at the conclusion of a vacancy chain usually only a small, undesirable shell is left behind (Briffa, 2013; Chase, 2012; Chase et al., 1988; Laidre, 2012b; Lewis & Rotjan, 2009), often inadequate for even the evicted individual to enter (Laidre, 2014). What is referred to here as 'social timing' (joining conspecifics at the right time and place) is thus essential if crabs are to acquire a superior shell.

Animal social structures form at many scales (Sih, Hanser, & McHugh, 2009; Wey, Blumstein, Shen, & Jordan, 2008). For terrestrial hermit crabs, the fine-scale social structures that precede shell acquisition are prominently visible from afar, so these structured assemblies may provide highly informative predictors of potential shell opportunities. Prior experiments have revealed that terrestrial hermit crabs 'eavesdrop' (sensu Earley, 2010) on conspecific social gatherings, using the level of commotion within congregations to predict future evictions (Laidre, 2013a). However,

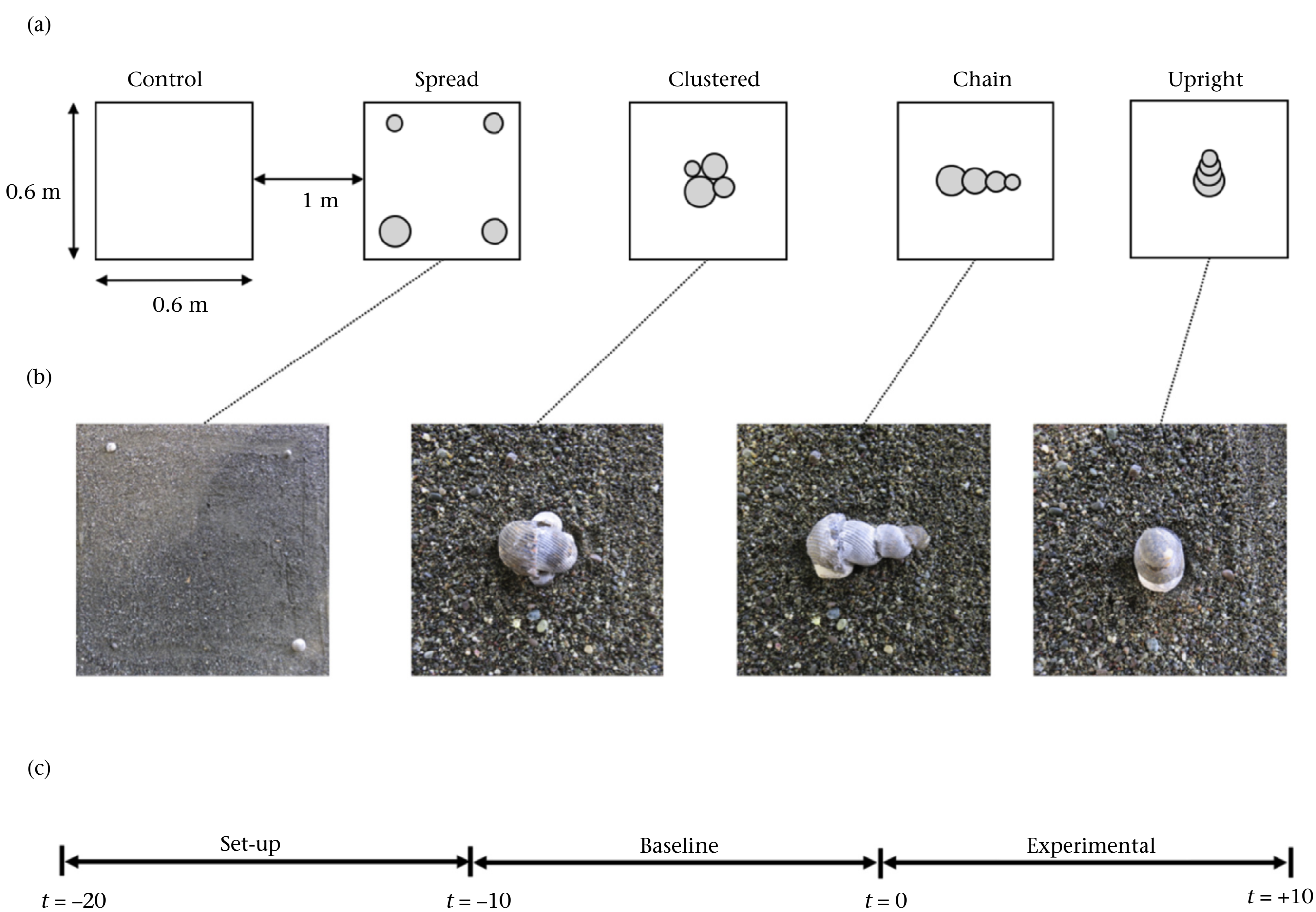

Figure 1. Spatial and temporal organization of experiments. (a) Spatial layout of quadrats, with order randomized across experiments. From left to right: quadrats show the temporary social structures that are formed by social hermit crabs during successive stages in the social shell-acquisition process. 'Upright' is a novel social structure. (b) Picture of each quadrat, with shells arrayed to mimic each social structure. (c) Experimental timeline (see Methods for details).