Measuring boldness in decapod crustaceans: an overview of methodological approaches and potential caveats

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Behaviours such as boldness (the willingness to take risks) vary within and among species and can influence fitness by indirectly affecting resource competition, mortality risk, reproductive success, and dispersal. As such, many studies have investigated boldness in decapod crustaceans, a group of considerable ecological and economic importance. An initial review of these studies suggested outcome inconsistencies that warrant an examination of the approaches used to measure boldness. Boldness is often quantified by measuring behaviours such as latency to emerge from a shelter, exploration of novel environments, or activity following a threat. Hence, we provide an overview of the growth of research and taxonomic representation and analyse the gaps in the methodological approaches for studies examining boldness in decapods over 20 years (2004 – 2024). An examination of 78 studies indicates steady growth that has been narrow in terms of subject taxonomy and methodologies to measure boldness. The outcomes of these studies are often affected by design choices such as the behaviours measured (some widely used, like shelter use, others more controversial, such as exploratory behaviours), the sex, age, condition, and origin of the subjects, and the experimental or rearing conditions (e.g., acclimation times, density, feeding regime, and temperature). Understanding how methodological choices influence decapod boldness is necessary to improve temporal consistency, ensure reproducibility and reliable comparisons among studies, thereby facilitating meta-analyses. Otherwise, inconsistent reporting of design choices may limit the accuracy and feasibility of such meta-analyses, hindering the synthesis of results.

1 Introduction

Communities are largely shaped by complex interactions between organisms, for which behaviour can play a key role (Gilman et al., 2010; Nagelkerken and Munday, 2016). Behavioural tendencies that vary among individuals in a manner that is consistent over time and across contexts are referred to as personality traits (Gosling, 2001; Biro and Stamps, 2008). Several personality traits have been identified, including exploration, aggressiveness, activity, sociability (Gosling, 2001; Rádai et al., 2022), and boldness or the willingness to take risks (Ward et al., 2004). Consistent differences in behaviour can be found not only among individuals but also among related species (Linzmaier et al., 2018). So unsurprisingly, traits like boldness have been widely studied due to their implications for foraging (Maskrey et al., 2018), reproductive success (Gruber et al., 2019), and survival (often in a trade off with foraging or mating benefits) (Belgrad and Griffen, 2016). Boldness has also been linked to agonistic interactions such as aggression, known to be important in both natural and man-made aquaculture settings (Su et al., 2022a, b; Pintor et al., 2008; Sun et al., 2024). In the context of biological invasions, boldness is also relevant since bold behaviour can be associated with dispersal tendencies that might favour invasiveness (Fraser et al., 2001; Damas-Moreira et al., 2019).

Understanding behavioural traits such as boldness is important considering that it may reflect wider ecological and evolutionary divergence among lineages. However, the study of boldness in groups like decapod crustaceans is rather recent (Gherardi et al., 2012). In fact, between 2002 and 2011, boldness was studied in only five crustacean species: European hermit crabs (*Pagurus bernhardus*), fiddler crabs (*Austruca mjobergi* and *Leptuca pugilator*), and crayfish (*Astacus astacus* and *Pacifastacus leniusculus*) (Pratt et al., 2005; Pintor et al., 2008; Gherardi et al., 2012). This is surprising considering the importance of a group that includes a variety of keystone species, ecosystem engineers, and invasive species (Pintor et al., 2008; Reisinger and Lodge, 2016; Kabalan et al., 2024). For example, some crab species are keystone or top predators in coastal food webs (Kotta et al., 2018), exerting direct and indirect effects on associated benthic communities (Silliman and Bertness, 2002; Quijón and Snelgrove, 2005a, b; Kotta et al., 2018; Young and Elliott, 2020). Similarly, various invasive crabs alter ecosystems worldwide by out-competing or consuming native species (Epifanio, 2013; Ens et al., 2022) or by disrupting habitats or habitat-forming-species (Bissett et al., 2025).

Despite the existing body of research on boldness, there is a growing number of inconsistent outcomes (Watanabe et al., 2012; Hills and Webster, 2022) that warrant an examination of the methodological approaches being used to study this behavioural trait. We address this by examining published studies on boldness in decapod crustaceans over a relevant period (20 years, 2004 – 2024), focusing on the growth of this research, the subjects (species) used, their characteristics and origin, and the experimental conditions of the behavioural trials. We examined 78 studies, focusing on the caveats that could prevent comparisons among species and studies and impede efforts to draw general conclusions about the influence of boldness on decapod ecology.

2 Search approach

We explored the literature on boldness in decapods by focusing on primary research articles published between January 1, 2004 and November 8, 2024 (20 years). The articles were obtained by searching the Web of Science database, using the following generic search terms: [Topic = (risk-taking OR bold* OR shy*) AND (decapod* OR crab OR lobster OR crayfish OR prawn OR shrimp) AND behaviour*] AND [Publication Date = 2004-01-01 to 2024-11-08]. An initial set of articles included 163 studies, but those that did not directly (explicitly) quantify boldness or risk-taking behaviours (*n* = 85) were subsequently excluded. A total of 78 articles were therefore retained from this process and thoroughly examined in the review.

3 An overview of boldness in decapod crustaceans

3.1 The growth, taxonomic focus and measurement of boldness in decapods

The number of studies published on boldness in decapods has increased consistently since 2004, reaching 78 articles by November 2024 (Figure 1A). Such growth likely reflects the parallel increase in the number of studies in the broader field of animal personality traits, for which some of the species referred to below have been used as models. To-date, research on boldness in decapods has focused on crayfish (21 articles), Anomuran crabs (24 articles), Brachyuran crabs (26 articles), and shrimp and prawns (7 articles) (Figure 1B), from a variety of freshwater, marine, brackish, and terrestrial habitats (Decker and Griffen, 2012; Reisinger et al., 2020; Zhu et al., 2022; Sakich et al., 2023). Hermit crabs (Anomura in Figure 1B) have accounted for nearly 31% of these studies, with most of these (~22% of total) focusing on one species, the marine European hermit crab (*Pagurus bernhardus*). Crayfish and Brachyuran crabs were also commonly studied groups, accounting for approximately 27% and 33% of the studies, respectively. Notably, our analysis confirms no boldness studies on lobsters exist as of November 2024, despite the ecological and commercial importance of this diverse group of crustaceans (Boudreau and Worm, 2012). The lack of boldness studies on lobsters likely relates to handling constraints and space feasibility, as large, highly mobile animals require bigger tanks or mesocosms, challenging the measurement of natural behavioural responses (see Polverino et al., 2016).

Boldness has most often (~81% of studies) been assessed by measuring shelter use (Tables 1, 2), using the underlying assumption that reduced shelter use is bold behaviour since it entails an increase in mortality risk (Belgrad and Griffen, 2018).
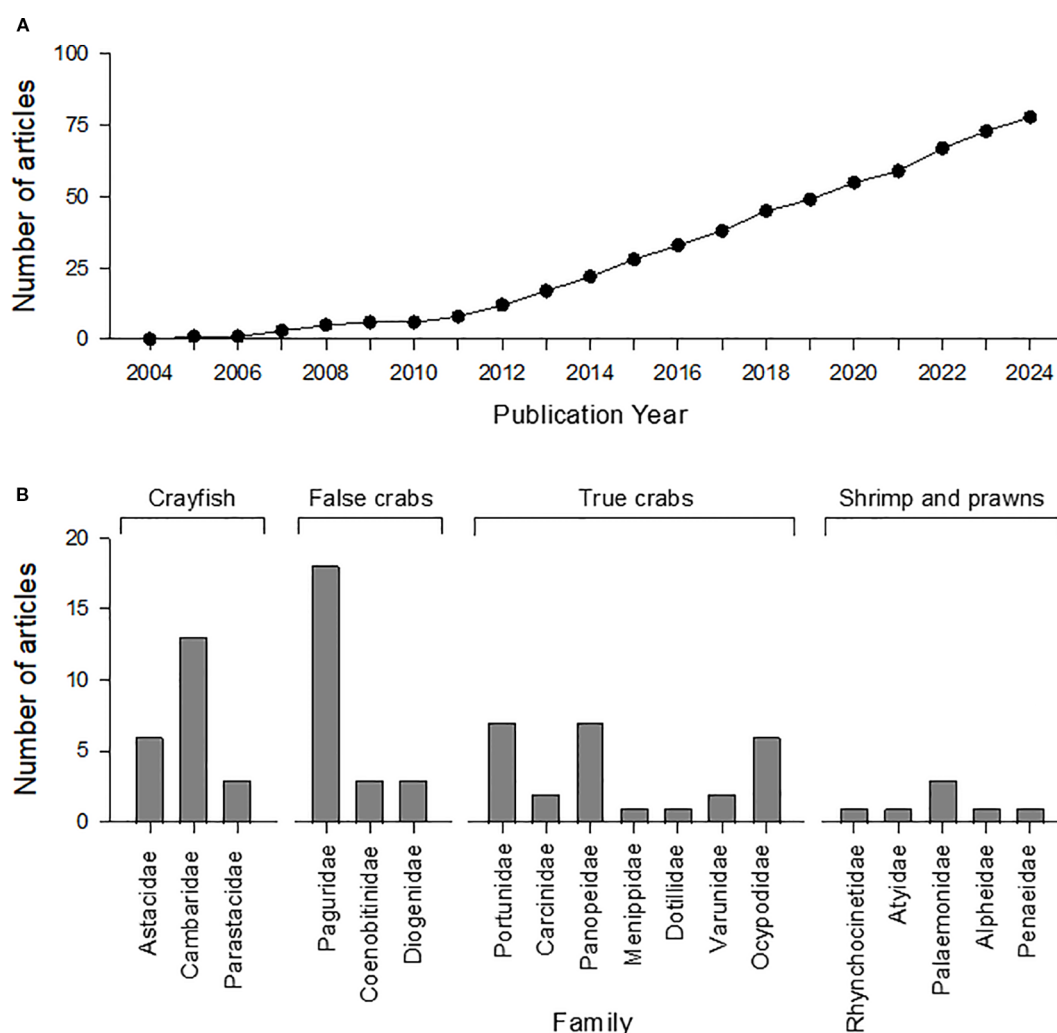
FIGURE 1
(A) Cumulative number of primary research articles on boldness in decapod species over two decades (January 1, 2004 to November 8, 2024).
(B) Allocation of articles on boldness in decapods across families and common groups.

Measures like latency to emerge from shelter or the proportion of time spent using shelter, particularly following a threat, are among the most popular. For example, all studies on hermit crabs measured shelter emergence (i.e., startle response duration) to assess boldness (Table 2), since the crabs' own shell acts as a shelter. Furthermore, minimally invasive shelter use tests can be conducted using existing shelters in the field (e.g., burrows for fiddler crabs; Reaney, 2007). These measures are also simple, repeatable, and applicable on a wide diversity of species. However, the species' natural behavioural patterns should be considered when selecting a boldness measurement. Measurements of latency to emerge may overestimate boldness in species with less shelter dependence, such as some swimming crab species, or overestimate it in less active species that may sit for longer periods in a shelter, regardless of any direct response to a threat.

Even though most studies have relied on shelter tests to evaluate boldness (Table 2), the use of alternative methods seems wise for further research. Circumventing the issue of shelter dependence, boldness has been less frequently quantified using measurements of

exploratory tendencies (~8%; e.g., Maskrey et al., 2018), by comparing threat responses (~4% of studies; e.g., claw raising behaviour in crayfish, Galib et al., 2022), or by measuring activity such as foraging, mating, or locomotion, either during or after a threat (e.g., approach by a human or encountering predator cues; ~10% of studies; e.g., Ory et al., 2015; Marangon et al., 2020; Sbragaglia and Breithaupt, 2022). Though exploratory tendencies are well represented in animal personality research (e.g., Galib et al., 2022; Ferderer et al., 2022; Su et al., 2024), they could appear infrequently in our review partly because some of these studies do not explicitly describe it as boldness. Many studies acknowledge an exploration-avoidance axis as a distinct personality trait from a bold-shy axis, describing a subject's behavioural response to new environments or objects (Réale et al., 2007). However, these novel areas and objects could pose unknown threats, such that exploration is deemed risky and also considered boldness (Réale et al., 2007).

Out of all studies examined, only ~17% used multiple behavioural indices to quantify boldness (Table 2). For example, in studies using

TABLE 1 Summary of tests used to quantify and compare boldness using decapod species as subjects.

Test	Behaviours quantified	Examples (references)
Emergence test	Latency to emerge from shelter Time spent using shelter Distance travelled outside of shelter Duration of startle response (hermit crabs) (*) Latency to abandon shell (hermit crabs)	(Gorman et al., 2018; Heatwole et al., 2018; Liang et al., 2020; Zhu et al., 2023)
Exploration of a novel environment	Proportion of the area explored Distance travelled Distance from walls (e.g., thigmotaxis) Tendency to cross a barrier (e.g., number of crossing attempts, proportion of individuals that crossed, time required to cross)	(Decker and Griffen, 2012; Pârvulescu et al., 2021; Rickward et al., 2024; Sun et al., 2024)
Novel object	Latency to approach a novel object	(Ro et al., 2022)
Response to a predation threat	Latency to begin an activity (e.g., locomotion, feeding) Time spent active, foraging, or mating Latency to re-emerge after sheltering Latency to approach a region where a predator strike occurred Description and comparison of antipredator responses (e.g., fight, flight, or freeze behaviours)	(Reaney and Backwell, 2007; Pintor et al., 2008; Toscano, 2017; Linzmaier et al., 2018; Ferderer et al., 2022; Sbragaglia and Breithaupt, 2022)

(*) Duration of startle response corresponds to the time from threat cessation to normal activity resumption.

male fiddler crabs (*L. pugilator*), latency to re-emerge from a burrow following a threat (a human waving a towel) was positively correlated with the number of re-emergences after repeated threats before failing to re-emerge (Pratt et al., 2005). Though boldness can be temporally consistent within a given context (Sakich et al., 2023; Su et al., 2024), there is evidence that risk-taking might vary across distinct contexts (Decker and Griffen, 2012). For instance, if exploration in the absence of a threat is considered boldness, then its relationship with threat-related boldness measures can be used to test the context dependency of boldness. To this end, studies with female fiddler crabs (*L. pugilator*) showed that the latency to re-emerge from a burrow following a threat (i.e., human approach) was unrelated to the tendency to explore a novel environment (Decker and Griffen, 2012). Likewise, relationships between boldness and exploration were not detected in crayfish (*Cherax destructor;* Ferderer et al., 2022) or swimming crabs (*Portunus trituberculatus*; Zhu et al., 2023). However, these findings are equivocal given that in the European hermit crab (Mowles et al., 2012) and a crayfish (*Procambarus clarkii;* Su et al., 2024), exploration and latency to re-emerge from shelter were correlated across individuals.

Overall, these findings suggest the need for multidimensional approaches to evaluate boldness, including considering the context of the behavioural measure (e.g., threatening vs non-threatening contexts). Measuring multiple risk-taking behaviours using standard tests (e.g., emergence latency and response to novel objects) might also be necessary to ensure that what is being measured as boldness is a consistent personality trait that is discernible across multiple contexts. Until further, more compelling, evidence can be gathered, it is reasonable to propose such approach as a standard recommendation: Future studies should aim at assessing boldness across both (threat and non-threat) contexts to ensure reliability and ecological validity. In this regard, researchers must also be mindful that variability among contexts may be influenced by the subject's ontogeny or energy reserves as discussed in the next section.

3.2 The influence of subjects' size, stage and condition

Size and life stage are widely known to influence the behaviour of organisms (Toscano et al., 2014; Liang et al., 2020). Nonetheless, nearly 13% of the studies reviewed failed to report the size of the subjects under study, which risks the gathering of inconsistent results among otherwise comparable studies. The subjects' sizes may influence their risk perception or locomotor performances, indirectly affecting boldness scores. For example, in male swimming crabs, adults exhibited a shorter latency to exit a shelter than juveniles (Liang et al., 2020). Similarly, in mud crabs (*Panopeus herbstii*), the time spent sheltering was negatively correlated with body size, likely because larger individuals are generally less susceptible to predation (Toscano et al., 2014). These examples suggest that minimum reporting standards are clearly needed, as proposed in more detail below (see Section 4.2). Unlike those studies, larger European hermit crabs were less bold (i.e., displayed longer startle response duration) than smaller individuals. In this case, however, larger individuals occupied a sedimentary subtidal habitat with less refuge compared to the intertidal habitat used by juveniles, that has seaweeds and other complex microhabitats (Briffa and Archer, 2023).

In other species, however, there is opposing evidence that body size is unrelated to boldness measurements. For instance, body size does not affect foraging behaviour following a predator strike in crayfish (*C. destructor;* Ferderer et al., 2022), startle response duration in the hermit crab *Clibanarius symmetricu* (Garcia et al., 2020), sheltering behaviour in green crabs (*Carcinus maenas*) and mitten crabs (*Eriocheir sinensis*) (Brodin and Drotz, 2014; Fürtbauer, 2015), or the distance that fiddler crabs (*Leptuca terpsichores*) move away from burrows when mating (Heatwole et al., 2018). Furthermore, the relationship between body size and boldness may vary depending on the specific risk-taking behaviour

TABLE 2 Summary of the literature examined, including subjects (common and species names arranged by main groups illustrated in Figure 1, namely crayfish, Anomura and Brachyura, and shrimp and prawns), sex (M: male; F: female) and life stage (Adult; Juv: juvenile; BS: body size if provided instead of life stage), habitat of subject's origin, and acclimation (pre-trial) conditions, including source of animals (CS: commercial supplier or aquaculture; Field collected), holding time of field-collected subjects, setting and duration of acclimation in experimental set up and pre-experimental feeding regimen.

Subjects			Acclimation			Boldness			Ref
Name	Sex/ stage	Habitat	Source/ holding	Setting/ duration	Feed regime	Behaviours measured	#	Main findings	
Signal crayfish *Pacifastacus leniusculus*	M BS	Freshwater	CS n.a.	Lab 5 d	2/wk	Locomotor activity following threat, with and without food present	n.a.	Intraspecific variation in boldness is not consistent across contexts in this invasive species	1
Signal crayfish *P. leniusculus*	M/F BS	Freshwater	Field ≥24 h	Lab 5 min	Daily or 1/2d	Latency to emerge from shelter following threat	2	Boldness is positively related to activity and the motivation to disperse, but unrelated to weir-passage success	2
Signal crayfish *P. leniusculus*	M/F BS	Freshwater	Field 3 h	Field 10 min	n.a.	Description of threat responses	n.a./2	Boldness-exploration-climbing behavioural axis is positively related to dispersal in newly established and invasion front populations	3
Signal crayfish, *P. leniusculus*	M/F Adult	Freshwater	Field ≥2 wk	Lab 24 h	Daily	Latency to forage and # of worms eaten in 5 min, with vs without predator cues	n.a.	Boldness is positively correlated with voracity, aggression, and feeding. Allopatric invaders are bolder than those with sympatric congeners or native crayfish	4
Rusty crayfish *Faxonius rusticus*	M/F BS	Freshwater	Field >1 wk	Lab 2 min	n.d.	Latency to emerge from shelter following threat	3	Boldness increases with *Microphallus* spp. parasite load	5
Rusty crayfish *F. rusticus*	M/F BS	Freshwater	Field ≥2 wk	Lab 10 min	2/wk	Latency to emerge from shelter in a novel environment	n.a.	Leaf litter breakdown is higher in areas with less bold crayfish	6
Virile crayfish *Faxonius virilis*	F BS	Freshwater	Field <3 mo	Lab 2 min	AdL	Latency to exit a box within aquaria in the presence of predator cue	n.a.	Activity levels decrease following herbicide exposure in bold but not shy crayfish	7
Virile & rusty crayfish *F. virilis & F. rusticus*	M/F Adult /BS	Freshwater	Field ≥4 wk	Lab 5 min	2/wk	Latency to exit shelter	n.a.	Boldness is similar among *F. rusticus* populations and higher than *F. virilis*; it is also higher in native than non-native *F. virilis* populations	8
Crayfish, *Faxonius limosus* & *Pontastacus leptodactylus*	M Adult	Freshwater	Field n.d.	Lab 2 d	AdL	Records of approach and cross a ramp half submerged in a tank	n.a.	A successful invader (*F. limosus*) is bolder and has a higher maximum pinching force than the native species	9
Virile crayfish *F. virilis*	F Adult	Freshwater	Field n.d.	Lab 2 min	AdL	Description of threat responses	n.a.	Boldness measures in lab are linked to exploration / activity in the field and can predict the time spent in agonism struggling when tethered in field	10
Crayfish, *F. virilis, F. propinquus & F. rusticus*	M/F BS	Freshwater	Field ≤6 mo	Lab 15 min	AdL	Latency to emerge from shelter in presence of predator	n.a.	*Microphallus* spp. infection increases boldness. *Faxonius virilis* is less bold than *F. propinquus* and *F. rusticus*	11
Noble crayfish *Astacus astacus*	M/F Juv	Freshwater	CS n.a.	Lab n.a.	AdL	Latency to emerge / time out of shelter, with vs without predation threats	3	Boldness is negatively correlated with resource (shelter) holding potential but unrelated to relative chelae size	12
Common yabby crayfish, *Cherax destructor*	M/F Juv	Freshwater	CS n.a.	Lab 17 d	AdL	Tendency to use shelter (in the day and at night)	26/14	Boldness is positively correlated to foraging activity, growth, and possibly linked to life productivity. Males are bolder than females	13

(Continued)

TABLE 2 Continued

Subjects			Acclimation			Boldness		Results		Ref
Name	Sex/stage	Habitat	Source/holding	Setting/duration	Feed regime	Behaviours measured	#	Main findings		
Common yabby crayfish, *C. destructor*	M/F BS	Freshwater	Field 40 d	Lab 1 min	1/2d	Latency to forage in area struck by predator / time spent moving after threat / time inside strike zone	4	Boldness is not related to temperature, sex, body size, activity or exploration		14
Common yabby crayfish, *C. destructor*	M/F Juv	Freshwater	CS n.a.	Lab n.d.	AdL	Tendency to spend time out of burrow in an open area (in the day and at night)	13/5	Boldness, voraciousness, and growth are positively correlated. Harvest risk rises with night boldness. Fast growers might be at greater risk to fishing		15
Crayfish *F. rusticus*	M/F BS	Freshwater	Field n.d.	Lab n.a.	AdL	Proportion of individuals using shelter, with vs without predation threat (in the day and at night)	6/4	*Microphallus* spp. infection increases boldness and invertebrate feeding under predation threat		16
Red swamp crayfish *Procambarus clarkii*	M/F Adult	Freshwater	CS n.a.	Lab 5 min	2/d	Latency to emerge from shelter	3	Boldness is lower in crayfish reared at low density and is positively related to exploration regardless of density		17
Red swamp crayfish *P. clarkii*	n.d. Juv	Freshwater	CS n.a.	Lab 1 h	n.d.	Latency to escape the threat of being caught	8	Boldness increases with temperature and is negatively correlated with activity but not with aggressiveness		18
Red swamp crayfish *P. clarkii*	M/F Juv	Freshwater	Field 24 d	Lab 10 min	3/wk	Latency to exit a dark refuge into a light area	6	Boldness is repeatable over ontogeny, linked to larger and more arched chelae, but inversely linked to anxiety		19
Spiny cheek crayfish *Faxonius limosus*	M BS	Freshwater	Field ≤1 wk	Lab 5 min	AdL	Latency to emerge from shelter	n.a.	Environmentally realistic citalopram (SSRI) exposure increases boldness		20
Marbled & spiny cheek crayfish, *Procambarus virginalis* & *F. limosus*	M/F BS	Freshwater	Field/Lab; ≥1 mo/n.a.	Lab 30 min	AdL	Description of threat responses	3	*P. virginalis* tends to freeze whereas *F. limosus* is more likely to react offensively or defensively to a threat		21
European hermit crab *Pagurus bernhardus*	M BS	Marine	Field n.d.	Lab n.a.	n.d.	Duration of startle response	2	Smaller intertidal hermit crabs are bolder than larger subtidal crabs		22
European hermit crab *P. bernhardus*	M Adult	Marine intertidal	Field n.a.	Lab 24 h	AdL	Duration of startle response	8	Boldness is negatively linked to size of spermatophore, i.e. fecundity		23
European hermit crab *P. bernhardus*	M BS	Marine	Field n.a.	Lab 24 h	AdL	Duration of startle response	n.a.	Boldness is lower for crabs in conspicuous shells, but intraspecific variation in boldness is consistent across shell-substrate contrast levels		24
European hermit crab *P. bernhardus*	M Adult	Marine intertidal	Field 2 d	Lab 2 d	AdL	Duration of startle response	10	The predictability of boldness varies among individuals		25
European hermit crab *P. bernhardus*	n.d. BS	Marine	Field 1 or 28 d	Lab 5, 10, 30, or 60 min	1/2d	Duration of startle response	n.a.	Boldness is higher in crabs collected from the open (unsheltered) area and in crabs held in captivity for longer, but was unrelated to acclimation time		26

(Continued)

TABLE 2 Continued

Subjects			Acclimation			Boldness		Results		Ref
Name	Sex/stage	Habitat	Source/holding	Setting/duration	Feed regime	Behaviours measured	#	Main findings		
European hermit crab *P. bernhardus*	M BS	Marine rocky intertidal	Field n.a.	Lab 10 d	AdL	Duration of startle response	10	Boldness is unrelated to metabolic rate (MR), but intra-individual variation is negatively related to routine MR and positively to startle response MR		27
European hermit crab *P. bernhardus*	M Adult	Marine	Field n.a.	Lab 10 d	AdL	Duration of startle response (in the day and at night)	10/10	Light pollution could affect behaviour, since boldness is lower in crabs under constant light than 12:12 photoperiod		28
European hermit crab *P. bernhardus*	M BS	Marine intertidal	Field 1 d	Lab 1 h	AdL	Duration of startle response, with and without predator cues	4	Boldness decreases and intra-individual variation increases when predator cues are present		29
European hermit crab *P. bernhardus*	M/F BS	Marine rocky intertidal	Field n.a./<3 d	Field/Lab n.a./<1 d	n.a./AdL	Duration of startle response, with and without predator cues	n.a./2	Tests of behavioural consistency have greater effect sizes than those for plasticity		30
European hermit crab *P. bernhardus*	M BS	Marine	Field n.d.	Lab 16 h	n.d.	Duration of startle response	2	After adding a vacant shell, vacancy chains are longer for bolder groups; 1 d later, they are longer for shy groups		31
European hermit crab *P. bernhardus*	M BS	Marine rock pool	Field n.a.	Lab 16 h	AdL	Duration of startle response, with and without predator cues	n.a.	Boldness is correlated across low- and high-risk contexts, relates positively to exploration in both contexts, and to aggression in the low-risk context		32
European hermit crab *P. bernhardus*	n.d. n.d.	Marine	Field n.a.	Field/Lab n.a./~1 d	n.d.	Duration of startle response in shells of different quality (low vs high risk)	2	Across contexts, effect sizes for behavioural consistency are greater than for flexibility		33
European hermit crab *P. bernhardus*	M BS	Marine rock pool	Field n.d.	Lab n.d.	AdL	Duration of startle response	8	Startle response duration is not related to dynamic performance capacity		34
European hermit crab *P. bernhardus*	M/F n.d.	Marine	Field >3 wk	Lab 24 h	AdL	Duration of startle response	5	Boldness and predictability increase with microplastic exposure		35
European hermit crab *P. bernhardus*	M/F n.d.	Marine	Field n.d.	Lab 2 d	AdL	Duration of startle response	5	Exposure to copper reduces boldness but does not affect intra-individual variation or repeatability		36
European hermit crab *P. bernhardus*	M BS	Marine intertidal	Field n.d.	Lab 2/16 h	n.d.	Duration of startle response	2	Pre-fight boldness does not affect resource acquisition for attackers but is inversely linked to shell-defense. Post-fight boldness consistency drops in defenders but is similar in attackers		37
European hermit crab *P. bernhardus*	M BS	Marine intertidal	Field n.d.	Lab 24 h	AdL	Duration of startle response	8	Predictability is lower at a higher temperature		38
Caribbean hermit crab *Coenobita clypeatus*	n.d. n.d.	Terrestrial	Field/CS 1 h/n.a.	Lab 10/30 min	n.a./AdL	Duration of startle response / latency to right self and move after being flipped	4	Boldness rises with heat. Crabs from open areas are bolder than those from shade areas		39
Caribbean hermit crab *C. clypeatus*	n.d. BS	Terrestrial	CS n.a.	Lab n.d.	n.d.	Latency to hide & to re-emerge after threat / # trials to habituate to threat / latency to re-emerge after shock	2/n.a.	Some, but not all, behaviours are correlated across contexts within individuals		40

(Continued)

TABLE 2 Continued

Subjects			Acclimation			Boldness		Results		Ref
Name	Sex/stage	Habitat	Source/holding	Setting/duration	Feed regime	Behaviours measured	#	Main findings		
Hermit crab *Coenobita compressus*	M/F BS	Terrestrial	Field n.a.	Field n.a.	n.a.	Duration of startle response	2	Habitat disturbance is positively related to boldness, but not to repeatability or plasticity. In less disturbed areas, small crabs are bolder		41
Hermit crab *Clibanarius symmetricus*	M/F Adult	Mangrove	Field 24 h	Lab n.a.	n.d.	Duration of startle response	10	Boldness is not associated with microhabitat but is weakly positively correlated with exploration		42
Hermit crab *Clibanarius vittatus*	n.d. BS	Marine Mangrove	Field <1 d	Field/Lab n.a.	1/d	Startle response duration / latency to perform an abandonment response	n.a.	Predator or snail cues affect boldness differently depending on shell condition. Shell damage increases the chance of an abandonment response		43
Hermit crab *Calcinus californiensis*	M/F BS	Marine tropical shore	Field 1 d	Lab 2 h	1/d	Duration of startle response	2	Boldness is positively associated with a tendency to start and win fights in both sexes and fighting roles		44
Hermit crab *Pagurus tanneri*	n.d. n.d.	Deep sea	Field 1 mo	Lab 5 min	AdL once	Duration of startle response	3	Acidification does not affect boldness		45
Swimming crab *Portunus trituberculatus*	M BS	Marine	CS n.a.	Lab 10 min	Daily	Time spent out of shelter, with and without crab hemolymph in water	n.a./2	Bold crabs show higher consumption of O_2 and relative expression of Na+/K+-ATPase, 5-HT genes, lower hemolymph glucose and lactate contents		46
Swimming crab *P. trituberculatus*	M Adult/Juv	Marine .	CS n.a	Lab 10 min	Daily AdL	Latency to emerge from shelter	n.a.	Adults are bolder than juveniles, and boldness and aggressiveness are positively correlated only in adults		47
Swimming crab *P. trituberculatus*	M BS	Marine	CS n.a.	Lab n.a.	Daily AdL	Time spent out of shelter	n.a.	Boldness varies with time between feedings. Bold crabs are more likely to initiate fights		48
Swimming crab *P. trituberculatus*	M/F BS	Marine	CS n.a.	Lab 10 min	Daily	Time spent out of shelter	n.a.	Bold crabs are more likely to start a fight. Fights among bold crabs are longer and more intense. Bolder males have lower hemolymph glucose levels		49
Swimming crab *P. trituberculatus*	M BS	Marine	CS n.a.	Lab 10 min	Daily AdL	Time spent out of shelter	n.a.	Bold crabs are more active, start and win more fights, and their hemolymph has lower glucose and higher lactate contents before fights than shy crabs		50
Swimming crab *P. trituberculatus*	M BS	Marine	CS n.a.	Lab 10 min	Daily	Time spent out of shelter	n.a.	Boldness is not associated with exploration but rises with territoriality		51
Swimming crab *P. trituberculatus*	n.d. n.d.	Marine	CS n.a.	Lab 10 min	Daily	Time spent out of shelter	n.a.	A new personality analysis method based on machine learning. Under stress, boldness is a more stable trait than activity or hesitancy		52

(Continued)

TABLE 2 Continued

Subjects			Acclimation			Boldness		Results		Ref
Name	Sex/ stage	Habitat	Source/ holding	Setting/ duration	Feed regime	Behaviours measured	#	Main findings		
Fiddler crab *Leptuca pugilator*	F Adult	Marine mudflat estuary	Field n.a. / 24-36 h	Field/Lab n.a./10 min	n.a.	Latency to re-emerge from burrow after threat / tendency to explore novel environments	2	Smaller individuals are bolder, but boldness is not associated with hepatopancreas condition. Boldness was not correlated among contexts		53
Fiddler crab *L. pugilator*	M Adult	Marine marsh	Field n.a.	Field n.a.	n.a.	Latency to re-emerge from burrow after threat / # of re-emergences	5	At high densities, courting males show higher boldness and more similar re-emergence times to neighbours		54
Fiddler crab *Austruca mjobergi*	M Adult	Marine coast	Field n.a.	Field n.a.	n.a.	Latency to emerge from burrow following threat	2	Boldness is positively linked to aggressiveness, surface activity level and mating success		55
Fiddler crab *A. mjobergi*	M/F Adult	Marine mudflat	Field n.a.	Field n.a.	n.a.	Latency to re-emerge from burrow following threat	n.a.	Boldness is lower when foraging or mating chances are low, but increases in courting males with females present		56
Fiddler crab *A. mjobergi*	M Adult	Marine intertidal mudflat	Field n.a.	Field n.a.	n.a.	Tendency to take shelter in burrow after threat / latency to re-emerge from burrow	n.a.	Boldness is higher with female presence, but is not altered by mating periods or density		57
Fiddler crab *Leptuca terpsichores*	M Adult	Marine	Field n.a.	Field n.a.	n.a.	Distance moved from burrow	n.a.	Male boldness increases with size of courting females, but does not change with age or presence of sand hoods		58
Mud crab *Panopeus herbstii*	M/F Adult	Marine oyster reef	Field 25 h	Lab 10 min	AdL /1 d	Tendency to use shelter with predator cues (vs control group)	n.a.	Boldness increases in group settings in shyer individuals. Behavioural plasticity increases with predation risk		59
Mud crab *P. herbstii*	M/F BS	Marine oyster reef	Field 1-2 d	Lab 15 min	n.d.	Tendency to use shelter, with and without predator cues	2	Boldness decreases with predation threat and increases with size. Boldness is more repeatable in the predator cue context		60
Mud crab *P. herbstii*	F Adult	Marine oyster reef	Field 1 d	Lab 10 min	n.a.	Tendency to use shelter	n.a.	Boldness is affected by season in low- but not high-quality habitats. Energy stores and season affect boldness		61
Mud crab *P. herbstii*	n.d. Adult	Marine oyster reef	Field ~1 d	Lab 15 min	n.d.	Activity level in the presence vs absence of predator cues	n.a.	High behavioural plasticity is linked to increased survival under a predator threat		62
Mud crab *P. herbstii*	M/F Adult	Marine oyster reef	Field 1 d	Lab 10 min	n.a.	Tendency to use refuge with predator cues (vs no predator cue control)	n.a.	Predator cues raise refuge use. Toadfish and blue crabs eat more shy and bold crabs, respectively		63
Mud crab *P. herbstii*	M/F BS	Marine oyster reef	Field < 1 d	Lab 1-3d	AdL daily	Tendency to be active (un-sheltered / moving) under predation threat (vs without a threat)	n.a.	There is no interactive effect of predation threat and activity on mussel consumption		64
Mud crab *P. herbstii*	M/F Adult	Marine oyster reef	Field 1 d	Lab 10 min	n.a.	Tendency to use shelter	n.a.	Interactions between personality and habitat quality affect crab mortality and recapture rates		65
Green crab *Carcinus maenas*	M/F BS	Marine	Field 2 mo	Lab n.a.	2/wk	Time spent near shelter	2	Bolder crabs have lower hemolymph density		66
Green crab *C. maenas*	M/F Adult	Marine	Field n.d.	Lab 30 min	AdL	Latency to approach a novel object	n.a.	Boldness was not affected by any stage of *Microphallus similis* infection, a native parasite		67

(Continued)

TABLE 2 Continued

Subjects			Acclimation			Boldness		Results		Ref
Name	Sex/ stage	Habitat	Source/ holding	Setting/ duration	Feed regime	Behaviours measured	#		Main findings	
Chinese mitten crab *Eriocheir sinensis*	M BS	Freshwater	CS n.a.	Lab n.a.	Daily	Number of attempts to cross a partition	2		Boldness is positively associated with exploration, aggression, and agonistic interactions	68
Chinese mitten crab *E. sinensis*	M/F Adult	Freshwater/ brackish	Field 4 wk	Lab 10 min	AdL daily	Latency to exit shelter	n.a.		Boldness and activity are positively correlated, a behavioural syndrome that may favour invasiveness	69
Rock crab *Ozius truncatus*	n.d. BS	Marine intertidal reef	Field n.a.	Lab 4 d	2/d	Latency to emerge from shelter and reach food	8/6		Mean boldness increases with temperature, but behavioural responses vary among individuals	70
Sand bubbler crab *Dotilla wichmanni*	M/F Adult	Marine coast	Field n.a.	Field 10 min	n.a.	Latency to shelter after threat and latency to re-emerge from shelter	5		There is no intraspecific variation in behavioural plasticity or boldness-foraging behavioural syndrome	71
Shrimp *Palaemon serenus & P. intermedius*	n.d. BS	Marine	Field n.d.	Lab 15 min	n.d.	Foraging activity and duration under predator threat vs its absence	2		Boldness during foraging increases with temperature but is not affected by acidification	72
Shrimp, Alpheidae & Goby, *Ctenogobiops feroculus*	n.d. BS	Marine	Field n.a.	Field 2 min	n.a.	Flight-initiation distance and latency to emerge from burrow after threat	3		Boldness is interdependent among mutualistic shrimp and gobies	73
Rock shrimp *Rhynchocinetes typus*	M Adult	Marine rocky reef	Field n.d.	Lab 10 min	AdL/daily	Mating behaviour in the presence vs absence of a predator	n.a.		Older males assess threats more prior to mating. Boldness is likely related to survival-reproduction trade-offs	74
Red cherry shrimp, *Neocaridina davidi*	M/F Adult	Freshwater	CS n.a.	Lab 2 min	1/2d	Exploration / freezing / thigmotaxis / shelter use / latency to approach food	≤3		The multivariate structure of variation in behaviour is not fully aligned with the expectations of the bold-shy axis	75
Rockpool prawn *Palaemon elegans*	n.d. BS	Marine rock pool	Field 48 h	Lab 1 min	2/d	High-risk exploration when shelter is available	3		Boldness is negatively associated with resource holding potential (feeding duration)	76
Rockpool prawn *P. elegans*	M/F n.d.	Eelgrass, algae, sand	Field ≥1 wk	Lab 1 min	1/wk	Latency to feed following fright response	2		Fright response is positively correlated with shoaling tendency and negatively with exploration	77
Prawn *Penaeus (Penaeus) monodon*	n.d. Juv	Marine	CS n.a.	Lab 5 min	Daily	Time spent in center vs edge of container	n.a.		Dietary mercury exposure is unrelated to boldness	78

References: [1]Sbragaglia and Breithaupt, 2022, [2]Daniels and Kemp, 2022, [3]Galib et al., 2022, [4]Pintor et al., 2008, [5]MacKay and Moore, 2021, [6]Kabalan et al., 2024, [7]Steele and Moore, 2019, [8]Reisinger et al., 2020, [9]Pârvulescu et al., 2021, [10]Edwards et al., 2018, [11]Reisinger et al., 2015, [12]Vainikka et al., 2011, [13]Biro et al., 2014, [14]Ferderer et al., 2022, [15]Biro and Sampson, 2015, [16]Reisinger and Lodge, 2016, [17]Su et al., 2024, [18]Zhao and Feng, 2015, [19]Raffard et al., 2017, [20]Reisinger et al., 2021, [21]Linzmaier et al., 2018, [22]Briffa and Archer, 2023, [23]Bridger et al., 2015, [24]Briffa and Twyman, 2011, [25]Stamps et al., 2012, [26]Hills and Webster, 2022, [27]Velasque and Briffa, 2016, [28]Velasque et al., 2023, [29]Briffa, 2013a, [30]Briffa et al., 2008, [31]Briffa, 2013b, [32]Mowles et al., 2012, [33]Briffa and Bibost, 2009, [34]Courtene-Jones and Briffa, 2023, [35]Nanninga et al., 2020, [36]White and Briffa, 2017, [37]Courtene-Jones and Briffa, 2014, [38]Briffa et al., 2013, [39]Sakich et al., 2023, [40]Watanabe et al., 2012, [41]Hewes and Chaves-Campos, 2018, [42]Garcia et al., 2020, [43]Gorman et al., 2018, [44]Plasman et al., 2024, [45]Kim and Barry, 2016, [46]Zhu et al., 2022, [47]Liang et al., 2020, [48]Su et al., 2022a, [49]Su et al., 2022b, [50]Su et al., 2019, [51]Zhu et al., 2023, [52]Yang et al., 2020, [53]Decker and Griffen, 2012, [54]Pratt et al., 2005, [55]Reaney and Backwell, 2007, [56]Reaney, 2007, [57]Gruber et al., 2019, [58]Heatwole et al., 2018, [59]Belgrad and Griffen, 2017, [60]Toscano et al., 2014, [61]Belgrad et al., 2017, [62]Toscano, 2017, [63]Belgrad and Griffen, 2016, [64]Toscano and Griffen, 2014, [65]Belgrad and Griffen, 2018, [66]Fürtbauer, 2015, [67]Ro et al., 2022, [68]Sun et al., 2024, [69]Brodin and Drotz, 2014, [70]Biro et al., 2013, [71]Chen et al., 2019, [72]Marangon et al., 2020, [73]Polverino et al., 2024, [74]Ory et al., 2015, [75]Rickward et al., 2024, [76]Maskrey et al., 2018, [77]Chapman et al., 2013, [78]Harayashiki et al., 2016.

We also include boldness behaviours measured and number of repetitions per individual (#), main findings, and references (Ref; cited at the bottom of the Table). Note: n.d.: no data; n.a.: not applicable. Cited species names have been updated here based on accepted names in World Register of Marine Species (WoRMS: https://www.marinespecies.org/index.php) accessed in June 2025. Accepted and synonymous names for each major group include crayfish: *Faxonius virilis* (formerly, *Orconectes virilis*); *Faxonius propinquus* (formerly, *Orconectes propinquus*); *Faxonius rusticus* (formerly, *Orconectes rusticus*); and *Faxonius limosus* (formerly, *Orconectes limosus*); fiddler crabs: *Leptuca pugilator* (formerly, *Uca pugilator*); *Austruca mjobergi* (formerly, *Uca mjobergi*); shrimp: *Neocaridina davidi* (formerly, *Neocaridina. heteropoda*); and prawns: *Penaeus (Penaeus) monodon* (formerly, *Penaeus monodon*).

being analyzed. For example, two measures of boldness in fiddler crabs (*L. pugilator*), latency to re-emerge and the number of re-emergences following repeated threats, were unrelated to body size (Pratt et al., 2005), even though small females of the same species spent less time sheltering and were more exploratory than larger individuals (Decker and Griffen, 2012). The effect of body size on boldness thus seems to be species, context, and sex- dependent, so studies should always aim to accurately report subject life stage, size range, and sex.

The condition of experimental subjects is also critical to the evaluation of boldness, and aspects like feeding regimes or parasite burden (see below) are directly relevant to condition. While some studies fed subjects *ad libitum* and omitted a fasting period (Biro and Sampson, 2015; Bridger et al., 2015), others interrupted feeding (often for 24 hours) prior to measuring boldness (Toscano and Griffen, 2014; Belgrad et al., 2017; Liang et al., 2020). Unfortunately, approximately 36% of studies did not clearly report on how they standardized hunger levels prior to trials, either by providing food *ad libitum* or having a standardized fasting period. In the male swimming crab, measurements of boldness (i.e., proportion of time spent using a shelter) varied with time between feedings (or hunger level; Su et al., 2022a). Compared to crabs fed daily, those fed every 3 days exhibited higher boldness and those fed every 6 days were the least bold (Su et al., 2022a). Furthermore, well-fed Asian shore crabs (*Hemigrapsus sanguineus*) are known to feed less in bright light compared to dark conditions, likely to avoid predation (Spilmont et al., 2015). However, individuals fasted for 7 days did not avoid light (Spilmont et al., 2015), suggesting that they were bolder. Even though hunger levels might affect boldness, there is still little research addressing the impact of now "standard" fasting periods on the measurement of boldness.

Behavioural studies avoid using individuals with visible parasites (e.g., Bridger et al., 2015) because infected subjects (hosts) can change their behaviour and likely introduce variability in the measurement of boldness (Reisinger et al., 2015; Reisinger and Lodge, 2016). Many decapods, however, have parasites that are not externally visible (Martin et al., 2024). For instance, crayfish species serve as intermediate hosts of trematodes of the genus *Microphallus*, which encyst in their hepatopancreas (Sargent et al., 2014). The load of *Microphallus* parasites has been positively correlated with boldness (i.e., latency to emerge from shelter after alarm cue exposure) in the rusty crayfish (*Faxonius rusticus*) (MacKay and Moore, 2021). *Microphallus* spp. infections have also prompted the northern clearwater crayfish (*Orconectes propinquus*) and the virile crayfish (*O. virilis*) to reduce shelter use by ~40% and 15%, respectively, while increasing shelter affinity in the rusty crayfish by 11% (Reisinger et al., 2015). The same parasites increased the boldness (i.e., reduced latency to emerge from shelter under predation threat) of male crayfish of three species (*O. propinquus*, *O. virilis*, and *F. rusticus*). The only known counterexamples to parasite-induced behavioural change come from the invasive green crab, a species in which the infection by *Microphallus similis* did not alter the latency to approach a novel object (Ro et al., 2022), nor its time using a shelter or its foraging rates (Blakeslee et al., 2015). These authors suggested that since the

green crab has a very limited coevolutionary history with the parasite, this could explain why behaviour was not affected.

The existing research suggests that parasite-driven changes in behaviour (specifically boldness) has the potential to reshape how infected individuals (hosts) and related species interact (Friesen et al., 2020). For example, larger and bolder crayfish infected with trematodes tend to leave sheltered habitats more frequently, a behaviour that may increase exposure to infection (by increasing contact rates; see Lafferty and Shaw, 2013). This may, in turn, increase the efficacy of crayfish as an intermediate host for parasite transmission, with indirect effects on community dynamics. Behavioural interactions likely vary depending on the load or severity of the parasite infection and the ability of the host to manage those parasites. Despite its importance, nearly 74% of the studies compiled in Table 2 did not mention screening for parasites. At a minimum, future studies on behaviour in general – and boldness in particular – should include non-invasive screening for parasites (e.g., Courtene-Jones and Briffa, 2023), especially for taxa known to be at high-risk of infection. When feasible, a post-trial assessment of parasite burden should also be conducted (e.g., Reisinger et al., 2015). The integration of parasite detection protocols into behavioural studies will warrant more accurate results and advance our understanding of the impact of parasites on coexisting species and communities.

3.3 The influence of subjects' origin, status and holding time

Whether the subjects used in boldness studies are wild-caught or reared in captivity may have an influence on the outcome of boldness measurements, but this has not been thoroughly examined. Linzmaier et al. (2018) studied the response of the marbled crayfish (*Procambarus virginalis*) to a threat (i.e., the approach of a human hand), and found that wild-caught crayfish were less likely to flee (37%), more likely to fight (15%), and more likely to freeze (47%) than the aquarium-reared crayfish (62, 0, and 37%, respectively) (Linzmaier et al., 2018). This is relevant because differences in threat responses can be used to measure boldness in crayfish (Galib et al., 2022). The underlying causes of these differences may be selective forces that act upon behaviour in wild versus captive populations, due to the lack of natural predation threats in the latter (Huntingford, 2004). Animals bred for generations in captivity can develop differences from wild populations, which may be referred to as conditioning or behavioural plasticity but may also have a genetic basis (see Säisä et al., 2003; Blanchet et al., 2008). Whether the differences are ultimately linked to phenotypic plasticity or potential genetic differences likely depends on the species and rearing conditions. Regardless, these differences introduce an additional source of variation in the subject's behaviour that may be challenging to interpret but cannot be ignored.

The source population from which wild-caught individuals come from is another key aspect of their origin that could affect boldness, particularly for species with invasive populations (Pintor

et al., 2008). This is the case for the signal crayfish (*P. leniusculus*), in which boldness has been associated with behaviours like raising their claws in response to a threat (Galib et al., 2022). Individuals collected from populations at the frontline of their invasion were more likely to be classified as bold (~72% of individuals, *n* = 90) than individuals collected from newly established (~53%, *n* = 90) or fully established populations (~42%, *n* = 130) (Galib et al., 2022). These differences might be due to a link between boldness and the tendency of these animals to disperse, which is more pronounced in those at the front of an invasion process (Galib et al., 2022). Furthermore, invasive signal crayfish which were geographically apart from the native Shasta crayfish (*P. fortis*) were found to be bolder (i.e., exhibited shorter latency to forage under a predation threat) than those co-occurring with the Shasta crayfish, and even those found in their original distribution range (Pintor et al., 2008). These authors suggested that environmental differences, such as variations in prey availability, could lead to among-population differences in behavioural phenotypes. The presence of alternate predators, such as invasive or native counterparts, under low prey availability may also be a habitat -mediated selection pressure shaping personality traits (Pintor et al., 2008).

The habitat, or its resource quality, and the microhabitat (those found within a same, larger habitat) from where subjects are collected is another relevant consideration for boldness studies (Hills and Webster, 2022). For example, Sakich et al. (2023) measured boldness in Caribbean hermit crabs (*Coenobita clypeatus*) collected from either open and sunny microhabitats or shaded microhabitats within the same beaches. Hermit crabs from open microhabitats were bolder, exhibiting shorter startle responses and shorter times to self-flip and move after being placed upside down. Similar results were reported in European hermit crabs, as those collected from open microhabitats were bolder (i.e., shorter startle response durations) than those collected from beneath rocks or seaweeds (Hills and Webster, 2022). If bolder individuals spend less time using sheltered microhabitats, collecting experimental subjects from more visible, easily accessible (open) microhabitats could bias boldness measurements by excluding shyer individuals from the sample population. The quality of a given habitat is also known to affect the abundance of a species, likely causing local density-dependent changes in boldness (Belgrad and Griffen, 2017). Studies should therefore aim to sample individuals haphazardly across the species' habitat, including multiple microhabitats. Providing detailed descriptions of the methods used to collect subjects, rather than just a location, could also help determine if this is a potential source of subsequent conflicting results between studies.

Indirectly related to the collection of wild-caught subjects, is the amount of time they are held in captivity prior to boldness measurements, an aspect that approximately 15% of the studies examined failed to report (Table 2). This is relevant because this may bias boldness assessments (Hills and Webster, 2022). For example, in wild-caught European hermit crabs, individuals held in captivity for 28 days had a shorter startle response duration than those held for only 1 day (Hills and Webster, 2022). To our surprise, no other study examined had directly addressed the effect of time in

captivity on decapod boldness, and so, many studies seemed to assume a lack of any effects. These studies have reported that boldness within a context is consistent over time, implying that any impacts of holding time on behaviour were negligible. For example, the startle response duration in two hermit crabs (*Clibanarius symmetricus* and *P. bernhardus*) remained consistent at a given temperature, when tested daily for 10 and 8 days, respectively (Briffa et al., 2013; Garcia et al., 2020; see also Courtene-Jones and Briffa, 2023). Although it remains to be examined, the striking difference between these times and the 28 days lapse used by Hills and Webster (2022), may explain why boldness was not affected.

3.4 The influence of temperature and other experimental conditions

As ectotherms, ambient temperatures have large impacts on the biological processes of decapods and are well-known to influence behaviour (Briffa et al., 2013; Velasque and Briffa, 2016). Temperature is therefore a relevant component of the context in which boldness studies take place, yet approximately 32% of studies failed to report temperature records in some of their experiments. Empirical evidence on the impact of temperature on boldness is variable. Some studies indicate that an increase in temperature leads to an increase in boldness, whereas others have observed no effect (Biro et al., 2013; Marangon et al., 2020; Reisinger et al., 2020). Temperature may also affect intra-specific variation in boldness, as in European hermit crabs, for which the individual's duration of startle response was more variable at 15°C than at 10°C (Briffa et al., 2013). Since temperature affects the metabolic rate of ectotherms, changes in metabolic processes and energy needs might explain the effects of temperature on boldness as well (Briffa et al., 2013; Marangon et al., 2020). However, Velasque and Briffa (2016) reported that a measure of boldness (startle response duration) was not affected by metabolic rate in European hermit crabs. Future research should focus on disentangling the mechanisms by which temperature affects boldness in decapods, aiming to explain how this behavioural response changes (in direction, strength, or variation) with temperature alterations.

The density of subjects used in behavioural trials (individual versus multiple subjects) may further affect the outcome of boldness studies (Pratt et al., 2005; Belgrad and Griffen, 2017). For instance, in the mud crab (*P. herbstii*), shy individuals (i.e., those spending more time under a refuge) increased their boldness when conspecifics were present, though the refuge use of bold crabs was consistent regardless of the presence or absence of conspecifics (Belgrad and Griffen, 2017). Similarly, male fiddler crabs (*L. pugilator*) were also more likely to emerge from their burrows, along with neighbouring males, when population densities were high (Pratt et al., 2005). In these cases, population density seems to be associated with reduced predation risk, which could prompt increased risk-taking in the subjects (Pratt et al., 2005). Higher densities may also increase competition among subjects and prompt shy individuals to act more boldly to compete for limited resources

or mates (Reaney, 2007). Regarding the latter (mates), boldness has been shown to increase in males of two species of fiddler crabs, *L. pugilator* and *A. mjobergi*, during conditions linked to increased female activity and mating opportunities, though intra-individual variation in boldness in *U. pugilator* was consistent regardless of these conditions (Pratt et al., 2005; Reaney, 2007).

Density of subjects prior to experiments, such as during rearing, could also influence boldness (Su et al., 2024). For instance, individual crayfish (*Procambarus clarkii*) reared at high population densities were generally bolder at sexual maturity (i.e., exhibited a shorter latency to emerge from a shelter), than those reared at low density, possibly because boldness could improve an individual's competitive ability under increased intraspecific competition (Su et al., 2024). A contrasting case regarding the influence of density on boldness was provided by Gruber et al. (2019). These authors reported that population densities of male fiddler crabs (*A. mjobergi*) did not have an impact on boldness, measured as the tendency to take shelter and latency to re-emerge from burrows following a threat. Future research should focus on the cues used by decapods such as fiddler crabs to assess the presence of counterparts or their density, to attempt to standardize protocols while measuring boldness (Gruber et al., 2019).

As stated above, the core issue prompting our review was the growing number of inconsistent results among boldness studies (see e.g., Watanabe et al., 2012; Hills and Webster, 2022). As a result of the literature examined in sections 3.2 – 3.4 above, we offer an initial model (Figure 2) that attempts to integrate some key methodological variables and their interactions. While not comprehensive (many specific interactions are likely missing), the model illustrates context-dependent outcomes, that explain contrasting results among different subjects. This initial model may help researchers to identify which variables require concurrent controls in their experimental designs, for the species and conditions they choose to use in their trials.

4 Caveats and takeaways of two decades of boldness studies
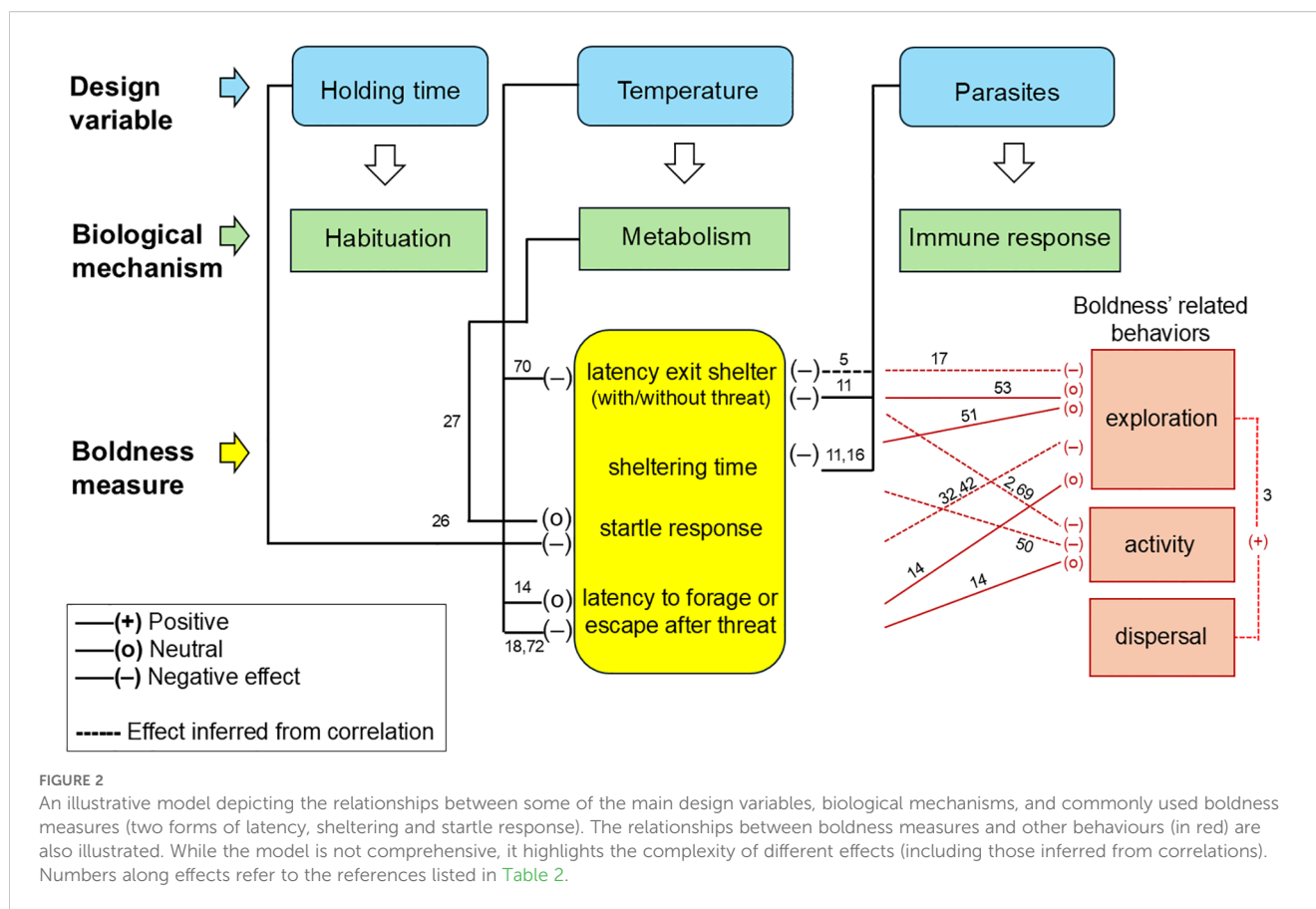
4.1 Most common caveats

A better understanding of boldness is critical given the importance of this personality trait on species fitness and ecological interactions (Belgrad and Griffen, 2016; Gruber et al., 2019; Sun et al., 2024). On a more applied context, for farmed species such as the Giant tiger prawn (*Penaeus monodon*), standardizing feeding protocols could shed light on key growth-cannibalism trade-offs, which are closely associated with boldness. Yet, this and other aspects discussed below were often not clearly reported (see Table 2). While the significance of this personality trait has been increasingly recognized, as evidenced by a steady growth in the number of studies on boldness (Figure 1A), there has not been a parallel increase in the diversification in the subjects (species) under study. As a result, most existing research is still confined to studies focused on a handful of species of e.g., hermit crabs and crayfish (see Table 2 for a compilation of studies).

Although the use of a few model species may favor comparability among studies, it also limits our ability to understand boldness more comprehensibly (Voelkl et al., 2020), by exploring a more diverse array of subjects across decapod taxa. For example, commercial species such as lobsters and crabs remain underrepresented, even though understanding boldness in some of these species may provide much insight into the key ecological roles they play in many communities (e.g., Silliman and Bertness, 2002; Kotta et al., 2018; Young and Elliott, 2020).

Beyond the diversity of subjects used, boldness has been measured in a variety of ways. However, an obvious caveat is the heavy focus on measurements of shelter use, and a lack of studies using two or more boldness indices concurrently. It is important to reiterate that different measures of boldness are only in some instances well correlated (Decker and Griffen, 2012; Watanabe et al., 2012), so an increase in the number of studies using multiple boldness measures will shed considerable insight on outcomes that until now appear inconsistent. Likewise, there is little doubt that the subject's sex, size, stage or condition (including hunger levels) has a strong influence on its (or their) behaviour and therefore on measured boldness levels. Yet, data on these aspects are still missing or not explicitly presented in many of the studies examined (Table 2). For example, 18% of the studies reviewed did not report subjects' sex, 13% of the studies did not report body size, and 9% of them did not clearly specify the subject life stage (either by stating adult vs juvenile or by reporting body size). The same applies to the subjects' origin, habitat or microhabitat of origin, or when applicable, the ecological (invasion) status, all of which may influence the outcome of boldness tests (see e.g., Decker and Griffen, 2012; Biro et al., 2013; Hills and Webster, 2022).

Since environmental factors (including rearing conditions) can drive variation in boldness (Sakich et al., 2023), they can also bias our interpretation and possible expectations regarding the interaction of these species with other individuals or species in natural settings. Yet, important details such as the time subjects were held in captivity prior to boldness tests was not explicitly stated in 15% of the studies, and the use of standardized hunger levels was not reported in 36% of the studies (Table 2). These interactions include but are not limited to competition (Liang et al., 2020) and aggressiveness or predation (e.g., Rossong et al., 2011, 2012). Factors like temperature (32% of the studies omitted reporting this in at least one of their sets of experiments) or the presence and number of conspecifics are also important conditions in an experimental setup measuring boldness. Therefore, more research should attempt to assess the influence of these factors before attempting to compare results among studies or among species. Recognizing what causes variation in boldness is critical to further understand the ecological and evolutionary consequences of risk-taking behaviours. Such behaviours, as stated before, dictate some of the main intra- and inter-specific relationships (e.g., Belgrad and Griffen, 2016; Maskrey et al., 2018) that ultimately contribute to coexistence and the structuring of communities. This also holds true for applied settings. For example, in studies quantifying boldness in aquaculture practices, boldness may become relevant for selective breeding, and in studies of invasive decapods, boldness may help to predict local impacts or prepare management measures.

FIGURE 2
An illustrative model depicting the relationships between some of the main design variables, biological mechanisms, and commonly used boldness measures (two forms of latency, sheltering and startle response). The relationships between boldness measures and other behaviours (in red) are also illustrated. While the model is not comprehensive, it highlights the complexity of different effects (including those inferred from correlations). Numbers along effects refer to the references listed in Table 2.

4.2 The takeaway: suggestions for a standardized measurement framework

Based on the existing evidence and the caveats discussed above, a brief set of guidelines can be proposed for future studies. While details on subjects and conditions would likely be species-specific, a general checklist on the reporting of the following parameters would clearly improve the quality of these studies and their comparability. As a minimum, boldness studies should consider: (a) Body size (average and range) and sex ratio of all experimental subjects; (b) An explicit statement of the application (or lack) of a starvation period prior to boldness measurement and its duration; (c) Parasite screening methods or a brief justification as to why this is not being applied; (d) A description of the relevant aspects of the habitats and microhabitat(s) from which the subjects were collected; (e) Acclimation times and the temperatures (or other physical parameters deemed important depending on subject species) used after collection and for experimental trials, and (f) Density in which subjects were raised or maintained before or during the boldness trials.

While generic, these guidelines should improve cross-study comparability, and more importantly, should remove the typical barriers associated with the partial reporting of the important methodological aspects that we have priorly identified as caveats. This may be especially useful if one of our recommendations – to diversify the number of species and types of species used as subjects – is given serious consideration. A broadening on the number of subjects (to include groups such as lobsters, to use an example

already discussed), will require added information on the adaptation of methodologies most often used for smaller crustaceans (such as hermit crabs). This may prevent the continued omission of some of the basic methodological parameters identified here. Due to their connections to other fields, research on boldness in crustaceans is expected to continue to drive the interest ecologists and behavioural biologists. An increased rigor on the reporting of the methodological parameters used in boldness studies would only strengthen its growth over the next couple of decades.

Author contributions

ED: Formal analysis, Investigation, Writing – original draft, Data curation, Writing – review & editing. PQ: Writing – review & editing, Data curation, Formal analysis. PR-B: Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation, Investigation, Funding acquisition, Writing – original draft.

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