Behavioral plasticity, behavioral syndromes and animal personality in crustacean decapods: An imperfect map is better than no map

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Abstract   Despite their key role as model organisms in many behavioral studies, crustacean decapods have been only slightly touched upon by the recent surge of scientific interest in animal personality. Only seven articles investigated the issue in a handful of species among hermit crabs, crabs, and crayfish. Obviously, a limited number of publications does not mean that personality is rare in decapods. On the contrary, few studies might be the result of a form of reluctance by behavioral ecologists to deal with such a phenomenon in these and other invertebrates. This reluctance contrasts with the enthusiasm shown in tackling the behavioral plasticity issue. Here we discuss the possible theoretical and methodological difficulties raised by applying the animal personality perspective to decapods and analyze implications of personality studies for their ecology, conservation, and welfare. By highlighting gaps in knowledge and directions of future research, our intention is to increase scientific emphasis on the issue [*Current Zoology* 58 (4): 567–579, 2012].

Keywords   Crustacean decapods, Behavioral plasticity, Animal personality, Behavioral syndromes, Conservation, Animal welfare

The early sailors knew their maps were not perfect, but imperfect maps were better than no map at all; it is in this spirit that we offer the present classification of animal personality, hoping that future researchers may find this initial sketch helpful in their quest for new discoveries (Gosling and John, 1999). Due to species richness (about 14,500 extant species so far described; De Grave et al., 2009), relatively large size of individuals and widespread availability, the crustacean order of Decapoda is one of the most studied invertebrate taxa in behavioral research. For decades, many species of crab, hermit crab, shrimp, lobster and crayfish have been used to test ethological theories of general relevance (e.g. sexual selection; Gherardi and Aquiloni, 2011). Investigation of a large number of behavioral phenomena (e.g. dominance hierarchies) has been often extended from vertebrates to these organisms (e.g. Gherardi, 2002, 2010). Knowledge of cognitive abilities in decapods has been refined (Gherardi, 2009) and concern about their capacity to experience pain has been raised (e.g. Elwood and Appel, 2009).

Notwithstanding their key role in behavioral studies, the recent surge of scientific interest in animal personality has only touched upon decapods. This is despite the evidence from early studies (Huntingford, 1976; Mather and Anderson, 1993) indicating that personality does not require a highly complex neural machinery, and recent research revealing the presence of consistent individual variation in many invertebrates, even including sea anemones (e.g. Gosling, 2001; Sinn and Moltschaniwskyj, 2005; Sinn et al., 2005; Briffa and Greenaway, 2011). Thus, published papers explicitly focusing on this phenomenon in decapod species are to date extremely scanty (Table 1), particularly if compared with the volume of the personality literature on non-human vertebrates (Fig. 1).

Obviously, as Gosling and John (1999, p. 74) metaphorically put it, "Antarctica will be discovered only if one sails south". So, a small number of studies on personality cannot be taken as a proof of its rarity in decapods. Instead, anyone who has, for example, handled enough crabs or crayfish intuitively knows that their reactions towards handlers differ on an individual basis with some being hyperactive and aggressive and others freezing; she/he has also noticed that such a different 'temperament' may persist in more than one behavioral context.

This review paper will attempt both to discuss the

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Table 1 A synthesis of the studies published on animal personality in crustacean decapods

#	Species	Infraorder	Term used	Behavioral axis
1	*Pagurus bernhardus*	Anomura	animal personality	shyness-boldness
2	*Pacifastacus leniusculus*	Astacidea	syndrome	aggressiveness
3	*Uca mjoebergi*	Brachyura	risk-taking behavior	shyness-boldness
4	*Pagurus bernhardus*	Anomura	animal personality	shyness-boldness
5	*Heterozius rotundifrons*	Brachyura	individuality	antipredator behavior
6	*Pagurus bernhardus*	Anomura	animal personality	shyness-boldness
7	*Astacus astacus*	Astacidea	personality trait	boldness

#	Behavioral assay/s	Comparisons between		Experiments in field/lab	Relationship with plasticity
		populations	species		
1	startle response	yes	no	field and lab	yes
2	aggression score, boldness to forage, threat response	yes	yes	lab	no
3	re-emergence time, time taken, distance traveled, number of fights to gain a burrow, number of active crabs, female choice	no	no	field	no
4	startle response	yes	no	field and lab	yes
5	catatony	no	no	lab	no
6	startle response	no	no	lab	no
7	latency to emerge time spent outside the shelter	no	no	lab	no

#	Consistency across			Adaptive value
	time	situations	contexts	analyzed
1	yes	yes: with/without predator cues	not analyzed	hypothesized
2	not analyzed	not analyzed	yes: across aggression, voracity, and boldness	no
3	not analyzed	not analyzed	yes: across boldness, aggression, and reproductive success	analyzed
4	yes	yes: different relative mass of shells	not analyzed	hypothesized
5	yes	yes: different number of predator cues	not analyzed	hypothesized
6	yes	yes: different conspicuosness of shells	not analyzed	hypothesized
7	yes	not analyzed	yes: between boldness and shelter ownership	hypothesized

#	Mechanistic Study aspects analyzed		Main aim/s of the study
1	not analyzed	Briffa et al., 2008	The balance between behavioral plasticity and animal personality.
2	not analyzed	Pintor et al., 2008	Higher aggressivity and activity and lower boldness in introduced crayfish living in sympatry with native crayfish.
3	not analyzed	Reaney and Backwell, 2008	Consistency of individual differences in risk-taking behavior across contexts.
4	not analyzed	Briffa and Bibost, 2009	Consistency of individual differences in startle responses within and across situations.
5	not analyzed	Hazlett and Bach, 2010	Consistency across time and situations.
6	not analyzed	Briffa and Twyman, 2011	Consistency of individual differences in startle responses between situations that vary in two factors.
7	not analyzed	Vainikka et al., 2011	Temporal repeatability and across-context consistency of individual differences in shelter use.
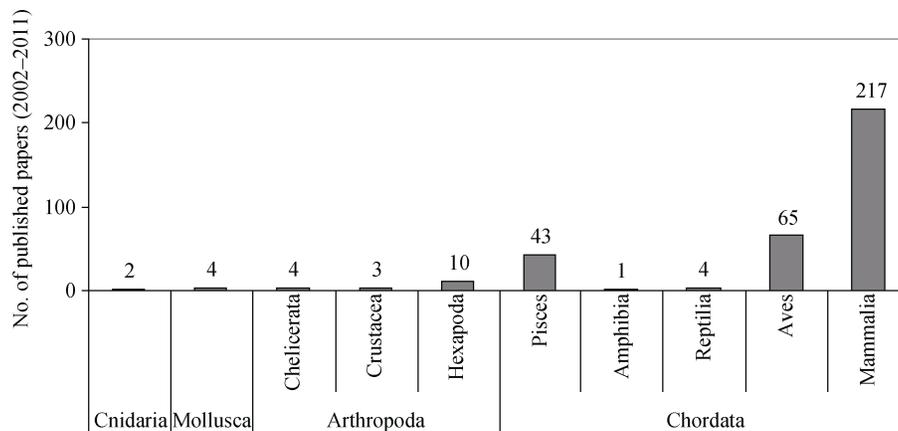
Fig. 1 Comparison among taxa for the number of scientific papers focused on animal personality published in the last decade, 2002 – 2011 (review papers are excluded)
Articles were searched on the ISI Web of Knowledge (http://apps.isiknowledge.com) database using the following search term combination: Title = (personalit* OR ((behavior* OR behaviour*) AND syndrome*) OR temperament* OR (coping AND style*) OR individualit*) AND Topic = (animal*).

reasons for the apparent reluctance by behavioral ecologists to deal with animal personality in decapods and to pinpoint new and profitable directions to be followed in future research. The few studies focused on personality in this taxon will be analyzed and compared with the more abundant literature on behavioral plasticity. Finally, we will discuss the implications of such studies for the ecology, conservation and welfare of decapods. By highlighting gaps in knowledge and directions of future research, we hope that our paper will stimulate increased scientific emphasis on the issue.

1 Behavioral Plasticity in Decapods: Benefits, Limits and Costs

Since the 1970s, biologists have been aware that a single genotype can produce more than one alternative form of behavior in response to environmental conditions (behavioral plasticity *sensu* West-Eberhardt, 1989). The obvious benefit gained by a plastic animal is that it can rely on a better behavior-environment match across more environments than would be possible by displaying a single behavior in all environments (Levins, 1968).

Due to the greater abundance of potential cues for regulating the expression of an 'immediate' (i.e. behavioral) adaptive response, behavioral plasticity was expected to evolve more readily than does any other form of phenotypic plasticity (West-Eberhardt, 1989). As a consequence, behavioral plasticity was acknowledged to play a prominent role in the initiation and amplification of phenotypic changes (West-Eberhardt, 1989) and behavior was assumed to act as the 'pacemaker' of evolu-

tion (Mayr, 1982).

1.1 Behavioral plasticity

The influence of behavioral plasticity on decapod behavior was enthusiastically investigated. It was recognized that behavior in this taxon is highly variable not only in species, population, sex and life stage, but also in individuals. Plasticity was attributed to a multiplicity of behavioral categories, from burrow construction by thalassinidean shrimp, including Cenozoic makers of the trace-fossil *Ophiomorpha nodosa* (Miller and Curran, 2001), to courtship behavior in the blue crab *Callinectes sapidus* (Bushmann, 1999).

Besides, some decapod species were shown to present alternative phenotypes in a single population, i.e. two or more forms of behavior and/or morphology which are not simultaneously expressed in the same individual (polyphenism *sensu* West-Eberhardt, 1989). Examples are the three morphological male types as shown in the freshwater prawn *Macrobrachium rosenbergii*. Types were distinguished by body size, relative claw length and claw color, i.e. 'small' males, SM (with the smallest body size and relative claw length, and light claws), 'orange claw' males, OC (with an intermediate body size and relative claw length, and orange claws), and 'blue claw' males, BC (with the largest body size and relative claw length, and blue claws) (Brody et al., 1980). Ra'anan and Sagi (1985) found that BCs and SMs show two alternative tactics of mating, while OCs are an intermediate stage between the two. Although superior in their mating tactic, BCs afford larger costs since they invest much energy in developing weaponry (large, massive claws), defending a territory, and pro-

tecting females. On the contrary, SMs practice a form of 'sneak copulation', taking advantage of their small body size and high mobility: they are inferior in physical encounters but waste little energy in generating weaponry.

Alternative behavioral forms not associated with morphotypes have been often documented in the use of space by, for example, several intertidal crabs of the Mictyridae and Ocypodidae families (e.g. Cameron, 1966; Wada, 1978; Zimmer-Faust, 1987). When sand-bubbler crabs *Dotilla fenestrata* emerge from their burrows with the receding tide, around 80% of large individuals wander about forming dense aggregations ('droves') that often move away from the normal residence zone (Gherardi and Russo, 1997). The remaining large crabs, along with small individuals, molting crabs and ovigerous females, are sedentary throughout most of low water and construct burrows of different architectures (either feeding-trench burrows or igloos), independently of the nature of the substrate (Gherardi et al., 1999). The type of the burrow conditions the inhabitant's behavioral budget and the timing of feeding activity. Single *D. fenestrata* crabs may 'switch' their spatial behavior from one tactic to the other in function of the richness in edible organic content of the substratum in the residential area (Gherardi et al., 2002). This form of behavioral plasticity (or behavioral flexibility *sensu* Piersma and Lindström, 1997; i.e. intra-individual and reversible behavioral transformation) was argued to be advantageous in that it allows crabs to respond to both the predictable and unpredictable elements of the intertidal environment (Ansell, 1988).

In the New Zealand crab *Heterozius rotundifrons*, the switch from one to another of three tactics of antipredator behavior (Hazlett and McLay, 2000, 2005) seems to be similarly advantageous. Upon disturbance, this species displays a 'catatonic' posture, consisting in remaining immobile with all limbs fully extended (Fig. 2). This posture may last 200 s on average in response to tactile inputs only; alternatively, it may be long (average duration: 325 s) when any intensity of a single category of danger signals was detected, or short (average duration: 110 s) when at least two categories of danger signals were detected (Hazlett and McLay, 2005). Catatonic posture is effective as an antipredator behavior because it acts as a physical impediment to be swallowed by predators (Hazlett and McLay, 2000). However, when crabs are subject to higher levels of predation risk (i.e. in the presence of multiple inputs), a short-time catatony is adaptive in that crabs get into a

shelter soon or move away from the highly dangerous area quickly, whereas staying in the same spot, even in the limb-extended posture, may favor predators. Crayfish species also display different tactics in antipredator behavior: crayfish cease all movement if they detect predator odor or alarm odor, but move rapidly when tactile input is added, and move further with tail flips when chemical and tactile cues are detected simultaneously (Bouwma and Hazlett, 2001).
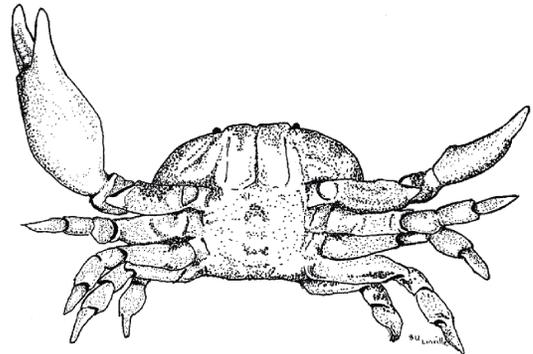
Fig. 2   Ventral view of a male *Heterozius rotundifrons* in which catatony has been induced (Hazlett and McLay, 2000). Reprinted from Animal Behaviour 59 (2000), pg 968, Figure 2, with permission from Elsevier (License Number: 2756361227270).

Finally, it was shown that individual experience, including differences in development conditions, may alter many aspects of decapod behavior, from the preference for given sizes of prey clams by the blue crab *C. sapidus* (Micheli, 1995) and the handling of novel shell types by the hermit crab *Calcinus tibicen* (Hazlett, 1995) to the intensity of agonistic behavior in hermit crabs and crayfish (Tricarico and Gherardi, 2007, 2010) and the type of avoidance reaction in crayfish (Fujimoto et al., 2011).

1.2   Limits and constraints of behavioral plasticity

With the integration of the behavioral plasticity perspective into decapod studies, it was assumed that the organisms exhibiting 'infinite' plasticity should be highly favored by evolution. In contrast, since the 1990s a number of studies has been showing that animals cannot consistently produce the optimum or else pay a large cost merely for the ability to be plastic (DeWitt et al., 1998). Hazlett (1995) was the first to raise the question of why behavioral plasticity is so limited in hermit crabs, among other decapods. Four mechanisms, he claimed, are responsible of such limitation. The first is the limited sensory capabilities of these organisms. For example, hermit crabs can smell octopuses and do modi-

fy both their shell choice when their odor is present (Brooks and Mariscal, 1985) and their placement behavior involving protective sea anemones (Brooks, 1989). On the contrary, they cannot detect the electromagnetic flux used by predator rays, which obviously limits plasticity in shell choice in areas of variable levels of predation by rays. Secondly, morphological constraints appear to be involved in the poor mating success of males of some hermit crabs species when occupying shells of a certain shape. For example, contrary to *Calcinus serauti*, males of *C. tibicen* and *Clibanarius zebra* cannot properly execute some precopulatory acts when in round-shaped shells because they cannot bend their ambulatory legs as far as can individuals of *C. serauti* (Hazlett, 1989; Hazlett and Baron, 1989). Memory capabilities may be also limited: the behavioral patterns that species of hermit crabs execute during agonistic interactions depend upon only the three acts executed previously (Hazlett and Bossert, 1965). An additional limitation of plasticity may be a consequence of the poor cognitive structure of decapods. For example, although *C. tibicen* and *Clibanarius vittatus* can detect the odor of conspecifics' hemolymph as a proxy of predation danger, they are incapable of associating such a smell with the size of the selected shell (Hazlett, 1995). Finally, as recently suggested by Briffa et al. (2008), such a surprisingly scarce extent of behavioral plasticity in hermit crabs among other decapods may reflect the existence in this taxon of personality traits that make their behavior relatively fixed throughout different contexts (but see Briffa and Bibost, 2009).

2 Studies on Personality and Behavioral Syndromes in Decapods

'Personality' is a term borrowed from psychology, where it refers to underlying behavioral tendencies that consistently differ across individuals. Terms such as 'temperament' and 'coping styles' were initially developed in separate literatures but their meaning has recently converged with the definition of personality (Gosling, 2001; Caspi et al., 2005; Koolhaas et al., 2007; Reale et al., 2007). In contrast, 'behavioral syndrome' refers to suites of correlated behaviors across multiple (two or more) observations (Sih et al., 2004a). In a broad sense, a behavioral syndrome involves behavioral consistency within individuals of a population over time (i.e. repeatability) and across situations and contexts (Bell, 2007a; Dall et al., 2004; Dingemanse and Réale, 2005; Sih et al., 2004a; Sih and Bell, 2008; Stamps and

Groothuis, 2010). Following Sih et al. (2004a), 'context' means here a functional behavioral category (e.g. feeding, mating, antipredator, parental care, contest, or dispersal contexts) and 'situation' is a given set of environmental or social conditions at one point in time (e.g. the presence or absence of predator risk). Within the syndrome, which is a property of a population, each individual shows a 'behavioral type', i.e. a particular configuration of behavior (e.g. more *versus* less aggressive individuals; Bell, 2007a; Sih et al., 2004a). Obviously, differences in behavioral patterns should be also consistent across measures of behavior (Briffa and Weiss, 2010). Based on the above definitions, personality and behavioral syndromes are not synonyms, as often reported in the literature, but, while any behavior that satisfies the criteria for a behavioral syndrome also satisfies the criteria for personality, the reverse is not always the case (Stamps and Groothuis, 2010; see also Groothuis and Carere, 2005).

2.1 Animal personality

Hermit crabs are the decapods in which consistent individual differences in behavior (hereafter referred to as 'personality'; see Mather and Logue, 2012) were analyzed for the first time and more extensively (Briffa et al., 2008; Briffa and Bibost, 2009; Briffa and Twyman, 2011). The 'shyness -boldness axis' (Wilson et al., 1994), often simply referred to as 'boldness', is the key axis of personality investigated here. A bold hermit crab will typically show high levels of exploratory behavior in a new environment and readily investigates novel objects. When disturbed, hermit crabs show a 'startle response' (e.g. Dingemanse et al., 2002; Brown et al., 2005), consisting in rapid withdrawals into the shell (Briffa and Elwood, 2001). Since startle responses are easily observable and their duration is inversely correlated with the boldness of individuals, they can be used as measures of boldness.

The advantages of using hermit crabs as model organisms for personality studies are several. First, startle responses can be elicited by means of a simple handling protocol. While this procedure does not remove the necessity of handling the animal (although in this case it is the gastropod shell rather than the hermit crab *per se* that is handled), it does mean that the animal is not placed into an artificial structure or subject to a stimulus that is far beyond its normal experience (hermit crabs can be handled by some predators, such as crabs). Second, startle response can be elicited in both the laboratory and field. Indeed, it is useful to know how behavior

varies in the animal's natural environment as this might be different from what happens in the laboratory. It is also possible to conduct experiments where responses are examined both *in situ* and in the laboratory context, allowing both an assessment of responses in a natural setting and experimental manipulation of situations. Besides, duration of startle responses can be accurately timed (from when hermit crabs are replaced on the substrate until they have reemerged to the point where walking legs are outside the aperture; Briffa et al., 2008). The fourth advantage results from hermit crabs being obligate occupants of portable refuges, most often in the form of empty gastropod shells (but see, e.g., Gherardi, 1996). The shells both protect the soft uncalcified abdomen from attacks by predators (Vance, 1972) and play a role in buffering against environmental extremes (e.g. Taylor, 1981). However, shells differ in their 'value' as a refuge to each single hermit crab in function of their shape, relative size, mass, and color. Shell value can be accurately assessed through shell selection experiments and any effects of such value on boldness measures can be easily accounted for (Elwood, 1995).

Studies on hermit crabs' personality addressed three general questions, i.e. (i) does boldness differ among individuals? (ii) if yes, are these differences consistent across time and situations? and (iii) what is the relative strength of behavioral plasticity and animal personality? The startle responses of *Pagurus bernhardus* were examined both *in situ* and across situations in the laboratory by manipulating the level of either the perceived predation risk (i.e. in the presence or absence of the odor of predator crabs *Carcinus maenas*; Briffa et al., 2008) or the extent of protection afforded by the occupied shell. The latter situation was achieved by supplying hermit crabs with shells of varying preferred mass (i.e. original shells and shells of either 75% or 100% of the preferred mass; Briffa and Bibost, 2009) or of different relative conspicuousness (i.e. dark brown and bright yellow shells against a light or a dark substratum; Briffa and Twyman, 2011). Interindividual differences in the duration of startling responses and their overall independence of discrete categories of individuals (sex and size) were always found, but average responses showed a significant variation between treatments, which indicates a certain ability by hermit crabs to modulate their behavior across situations, i.e. the existence of a form of behavioral plasticity. A significant pattern of individual consistency in behavior was also revealed by analyzing concordance in the ranks of individual startle durations between situations and across

time (Fig. 3). In any experiment, however, the extent of behavioral consistency largely exceeded behavioral plasticity between situations. This means that, although hermit crabs' behavior may be plastic, the costs and limits of plasticity cause hermit crabs to invest little in mechanisms required for an accurate modulation of responses between situations and on the contrary favor their reliance on 'approximately appropriate' responses based on behavioral consistency (Briffa et al., 2008).
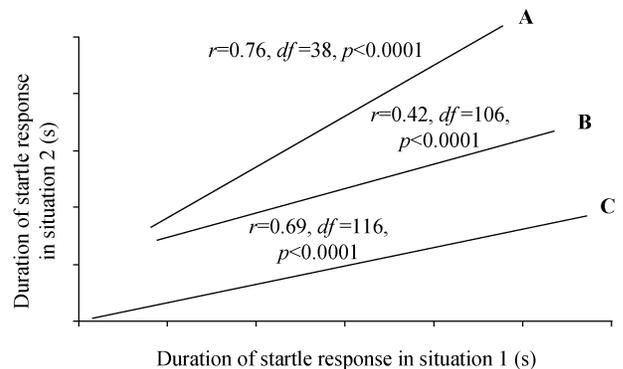
Fig. 3 Correlations (after Pearson test) between two situations for the duration of the startle response as an index of boldness in the hermit crab *Pagurus bernhardus*
Situations 1 and 2 are, respectively, low and high contrasts between shell color and background (**A**), occupancy by hermit crabs of their original shell in the field and in the laboratory (**B**), presence and absence of predator odors (**C**). Modified from: Briffa and Twyman (2011) (A); Briffa and Bibost (2009) (B); and Briffa et al. (2008) (C).

Boldness was the subject of study in the other decapods investigated so far for personality, i.e. the fiddler crab *Uca mjoebergi* (Reaney and Backwell, 2007), the Belliidae crab *H. rotundifrons* (Hazlett and Bach, 2010), and the noble crayfish *Astacus astacus* (Vainikka et al., 2011). Reaney and Backwell (2007) showed that 'risk-taking behavior' in the presence of a predator is an accurate behavioral predictor of male success in three unrelated contexts in *U. mjoebergi*. When confronted by predators, fiddler crabs rapidly retreat into their burrows. The time spent underground is costly in terms of missed foraging, courting, and mating opportunities, but rapid reemergence is risky because the threat may not have passed. Individuals must therefore play a 'waiting game' with the predator, deciding how long to delay reemergence and potentially expose themselves to another attack. Males were classified according to their risk-taking response when approached by a potential aerial predator: bold males were those willing to take greater risks and reemerge soon after a predation attack, whereas shy males remained in the safety of their burrows for longer. Individual variation in risk-taking be-

havior appeared to be consistent among individuals and was correlated to aggressiveness, activity levels, and mating success. Bold males were more likely to act aggressively toward other males. When searching for a new territory, bold males fought more territory holders than did shy males, who avoided fights by either evicting females or occupying empty burrows (Fig. 4). Risk-taking behavior appeared to be correlated with mating success: when given the choice between bold and shy males of similar size, females more often chose to mate with bold males. There may be several reasons for this. Bold males spent significantly more time active on the surface, whereas shy males spent longer periods of time in their burrows. Females would therefore be more likely to encounter bold males. Bold males also spent significantly more time courting females, which is likely to give them a mating advantage (Backwell et al., 1999). Furthermore, the behavior of mate-searching females may influence their selection of bold males: when receptive females move through the population in search of mates, they are constantly scared into nearby burrows by perceived threats but reemerge very rapidly. Bold males will therefore be the first potential mates that a female detects when she continues to search. Finally, a rapid reemergence time could reflect male's ability to escape predators and may be an honest signal of quality that females could use in selecting mates (Zahavi and Zahavi, 1997).


Fig. 4   The percentage of bold and shy males of the fiddler crab *Uca mjoebergi* that either fought a territorial male for a new burrow or avoided fights by either evicting a female or occupying an empty burrow
Modified from Reaney and Backwell (2007).

In *H. rotundifrons*, the limb-extended posture (or catatony) (see description in the section Behavioral plasticity: benefits, limits and costs) was used as a measure of boldness (Hazlett and Bach, 2010). Similarly to the startle response in hermit crabs, this posture

can be easily elicited by tactile stimulation. The duration of catatony (i.e. the time from placement on the sand to first limb movement) was measured upon repeated tactile induction within 10 min, upon three treatments (tactile induction alone; tactile induction and alarm odor; tactile induction, alarm odor, and exposure to a shadow) in one day, and upon tactile induction alone for five days. As a confirmation of the plasticity of this antipredator behavior (see the section Behavioral plasticity: benefits, limits and costs), duration varied among situations. However, crabs, independently of their sex or size, differed on an individual basis in being short-, intermediate or long-duration animals; besides, these interindividual differences were maintained across situations and over time (Fig. 5; Hazlett and Bach, 2010).
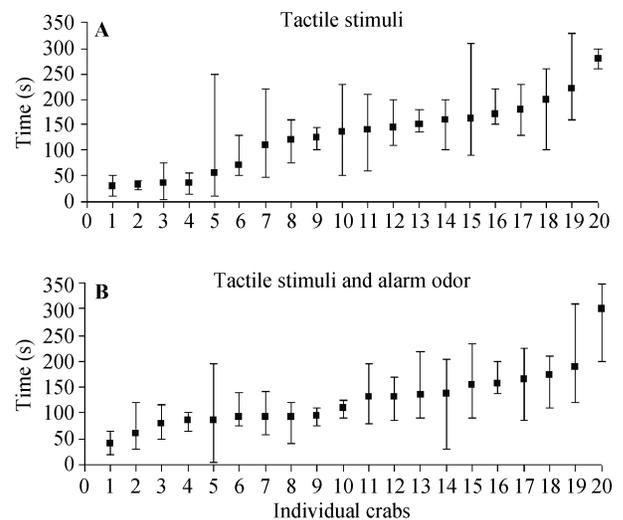
Fig. 5   Time spent in catatony by the crab *Heterozius rotundifrons* when stimulated five times in one day with tactile stimuli only (A) and tactile stimuli plus alarm odor (B)
The mean (■) and full range of values for each individual are shown. Modified from Hazlett and Bach (2010).

Finally, in *A. astacus*, the use of shelter was taken as a measure of boldness, low shelter use denoting high boldness and *vice versa* (Vainikka et al., 2011). In a first experiment (boldness test) each crayfish, after 3 days in an environment without predators or disturbance, was assigned to one of three treatment groups (exposure to predator odors, simultaneous exposure to predator odors and physical disturbance, and control) in the presence of a shelter and food in excess. In a second experiment (shelter possession test), pairs formed by size-matched individuals tested in the boldness test were placed in arenas that contained a single shelter under the exposure of predator odors. Individual crayfish, independently of the relative size of their chelae and of the treatment (Fig.

6), showed repeatable behaviors within and across periods of varying risk of predation, which suggests that boldness is a personality trait. In addition, behavior observed during the control period was consistent with the behavior observed in the shelter possession trials: individuals that were shy in the absence of predation risk occupied the shelter more often than their rivals, suggesting that in this species boldness is negatively correlated with resource holding potential (i.e. shelter possession under interference competition) (Vainikka et al., 2011).
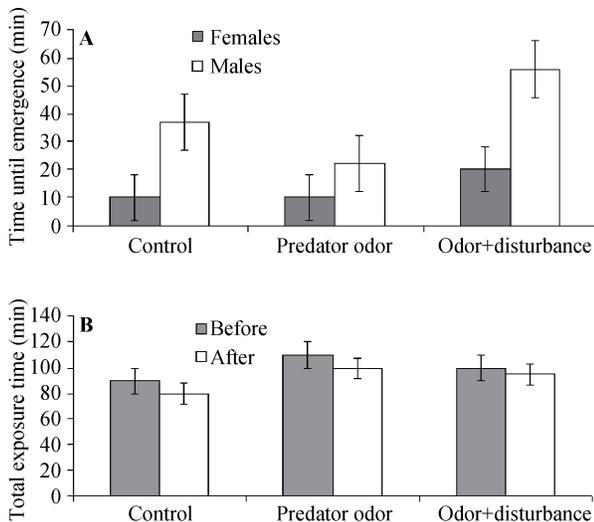
Fig. 6 Time until emergence from the shelter in females and males of the noble crayfish *Astacus astacus* (A) and total exposure times before/after the introduction (or sham introduction) of predator risk (B) in three treatment groups (control, predator odor, predator odor and disturbance)

Each observation period lasted 180 min. Bars denote mean values (± *SE*). Modified from Vainikka et al. (2011).

3   Why is Antarctica still far?

The reasons why research in animal personality has not yet been integrated into the literature on decapods, among other invertebrates, are diverse and include (i) reluctance to adopt the animal personality perspective, (ii) ambiguities in definitions, (iii) lack of a general framework, and (iv) difficulties in understanding the adaptive value of animal personality.

3.1   Reluctance to adopt the animal personality perspective

The integration of animal personality into behavioral studies has encouraged the rise of new views (Bell, 2007a), which may be difficult to accept when the study animal is a decapod. First, the focus on central tendencies, defined more than 20 years ago by Bennett (1987) as the 'tyranny of the Golden Mean', has become

meaningless and, in contrast, the interpretation of individual differences has shifted from a mere 'noise' around an adaptive mean to the essence (Careau et al., 2008; Williams, 2008). The reluctance to accept such a changed view may have been corroborated by both the difficulties in marking and following individuals for a substantial amount of time and the 'fear' of pseudoreplication.

Second, the animal personality perspective emphasizes carryovers across contexts and suggests that new insights will emerge from considering behavior in a more holistic way (Bell, 2007a). Holism in animal behavior clashes against the prevailing model according to which natural selection has favored different optima of different behavioral traits in different contexts. Behavior has generally been 'atomized' into single units (Gould and Lewontin, 1979) that are studied in different contexts as though they are independent of one another.

Finally, the study of some personality axes, such as the shyness-boldness axis, adds indeed "an interesting new dimension to behavioral ecology" (p. 442, Wilson et al., 1994). "Shyness-boldness is a behavioral *continuum* that cuts across the categories of age, sex, and size" (p. 442, Wilson et al., 1994), whereas the majority of behavioral ecologists has been used to focus on discrete categories for both behavior (e.g. alternative reproductive strategies) and individuals (e.g. age, sex, or size). As a consequence, theoretical difficulties in accepting this view may have led to a neglect of whether, how, and why individual decapods differ in their behavior.

3.2   Ambiguities in definitions

Newcomers to studies in decapod personality are faced with a multitude of definitions of personality (see Réale et al., 2007), from 'the combination of characteristics or qualities that form an individual's distinctive character' (Soanes and Stevenson, 2005) to 'those characteristics of individuals that describe and account for consistent patterns of feeling, thinking and behaving' (Pervin and John, 1997). Besides, except in Stamps and Groothuis (2010), the difference between the concept of personality and the concept of behavioral syndromes is not made explicit; specifically, it is not made clear that a critical marker of personality is the consistency of interindividual differences in behavior across contexts, and not only their repeatability across time and situations (but see Reaney and Backwell, 2007).

As reported by Gosling (2001), many definitions refer to both measurable elements and 'unobservables', or qualities that are difficult to measure. Terminology has been generally developed with humans in mind

(Groothuis and Carere, 2005), which may have created 'the specter of anthropomorphism' (Gosling and John, 1999). To fight anthropomorphism, a tendency has been to eliminate any psychological connotation from the terms used, with the result of speaking in a different language than the jargon used in the personality literature, with references to, for example, 'correlated behaviors' or 'individuality' (Reaney and Backwell, 2007; Hazlett and Bach, 2010). Similarly, terms like 'fear' or 'anxiety' do not correspond to the same psychological state in crabs and humans (Kagan and Snidman, 2004), and 'boldness' in some studies (e.g. Briffa et al., 2008) has been called 'risk-taking behavior' in other studies (Reaney and Backwell, 2007). Taken together, these terminological ambiguities may lead to the phenomenon of the 'ethological fallacy' (Briffa and Weiss, 2010), a variant of the 'jingle and jangle' fallacies identified in human personality research (Kelley, 1927; Block, 1995).

We are confident that research in decapod personality might be stimulated by developing a common dictionary composed by as much 'neutral' as possible terms. Researchers should be also careful in selecting and describing the studied variables to ensure their comprehensibility and comparability (Gosling, 2001).

3.3 Lack of a general framework

Newcomers to studies in decapod personality are also faced with the lack of a general framework needed to orient their research. It seems not to be a chance that the existing studies in decapods have adopted the so-called 'candidate behavior' approach (Bell, 2007a), with focus on a trait, the shyness-boldness axis, that has already been shown to form part of a syndrome in other species. As said above, boldness is relatively easy to measure by a set of correlated behavioral variables. We expect that future research in decapods will rely on complementary approaches, including the 'puzzling behavior', the 'bottom-up', and the 'ecological' approaches (Bell, 2007a), and will extend its focus on other personality traits, for which abundant data and reliable behavioral assays are already available, such as exploration-avoidance, activity, aggressiveness, and sociability (Réale et al., 2007).

Only recently attempts have been made to draw a reference scheme for studies in animal personality. An ecological framework composed of four steps has been suggested by Réale et al. (2007). First, behavioral tests should be developed to provide appropriate and standardized behavioral trait measures for the species studied. Second, the tests should be validated by looking at the relationship between the behavioral trait and other trait measures. In particular, relationships with traits of ecological importance would help understanding the ecological role of personality. Third, researchers should find a link between behavior variation and fitness differences within a population and thus estimate the ecological and evolutionary roles of personality. Finally, intra- and interspecies comparisons should be undertaken with the aim of understanding the role of personality at a broader scale. With the exception of Reaney and Backwell (2007), the current literature on personality in decapods has been restricted to the first step of such scheme, leaving ample opportunities for future research.

Additionally, further advances in the study of personality in decapods, among other invertebrates, are expected from research on its proximate mechanisms (Briffa and Weiss, 2010). For example, analysis of the link between hormonal underpinnings of social structures such as dominance hierarchies and consistent interindividual differences in aggressiveness might provide a better understanding of the association among experience, behavioral plasticity and personality constraints. Finally, theoretical studies focused on the interplay between behavioral plasticity and behavioral syndromes (Dingemanse et al., 2009) will be fuelled by empirical studies investigating the relative strength of the two phenomena in inducing, for example, boldness (Briffa et al., 2008).

3.4 Difficulties in understanding the adaptive value of animal personality

The final difficulty encountered by newcomers to studies in decapod personality is to address the critical question of "Why having a personality?". Intuitively, intraindividual consistency appears easier to explain: behavioral plasticity is the optimum, but it requires time and energy to entirely rewire the neural machinery and/or information about the immediate environment may be uncertain (see the Section Behavioral plasticity: benefits, limits and costs). Thus, individuals might be better when consistent in their behavior (Bell, 2007b). This line of reasoning, however, does not explain consistency in the duration of the anti-predator behavior in *H. rotundifrons* under exposure to stimuli denoting different levels of predation risk, when it would be instead more advantageous to switch at the individual level from long catatony at low risk to short catatony at high risk and *vice versa* (Hazlett and Bach, 2010). An individual that is consistently bold is going to end up eaten by a predator, whereas the optimal animal should be bold only when it makes sense to be bold, adjusting its

behavior when the situation changes. Similarly, it is difficult to explain why some crabs are, for example, always bolder than others (Hazlett and Bach, 2010). Natural selection will favor individuals with profiles that perform the best. If such profile is heritable and linked to survival or reproductive success, less 'fit' individuals will be removed from the population. That is, crabs that do not successfully avoid predation would not get a chance to transmit boldness to their offspring, which means that variation will eventually disappear from the population.

Such a difficulty in answering to the question of 'why having a personality' is shared by students of the other animal taxa. Only recently theoreticians have proposed models based on either constraints or adaptive views (i.e. trait correlations result from either constraints on the architecture of behavior or natural selection; Wilson et al., 1994; Dall et al., 2004; Sih et al., 2004a, b; Neff and Sherman, 2004; Stamps, 2007; Wolf et al., 2007, 2008), but the paucity of empirical data about heritability and fitness makes these models still mere hypotheses.

4 Conclusions: Expectations and Opportunities

While studies on human personality have given insights for the prediction of disease risk, job satisfaction, risk-taking behavior, and reaction to social stress (see references in Réale et al., 2007), we are aware that an intensification of research on this phenomenon in non-human animals, crustacean decapods included, will aid the comprehension of many aspects of their ecology, ethology and evolution, such as population dynamics and genetics, niche expansion, speciation, and social behavior (Réale et al., 2007).

The importance of animal personality for the applied fields of animal production (c.f. Huntingford and Adams, 2005), conservation and animal welfare is crucial. Ignoring personality traits may create serious methodological issues. For example, because shy crayfish are less frequently observed and are less trappable, differences in personality will introduce a bias in capture-mark-recapture studies if not controlled for (c.f. Wilson et al., 1994).

Personality could have significant implications for captive breeding and recovery programs of endangered species, such as the European white-clawed crayfish *Austropotamobius pallipes*: data from other taxa suggest that bold individuals in captivity have higher reproduc-

tive success but do have reduced survival, as found in studies with wild animals. The fitness of bold animals in captivity might reduce variation in personality traits and select for traits that are maladaptive when they are released back into the wild (McDougall et al., 2006). On the other hand, releasing only shy animals or training animals to be shy in the presence of predators may lead to an increase in survival but could have a negative impact on long-term reproductive success because, as shown in *U. mjoebergi* (Reaney and Backwell, 2007), shy animals may have lower fitness. Further research examining the relationship between personality and fitness, in both captive and wild animals, is therefore needed, as well as studies examining the flexibility of personality and behavioral syndromes to determine whether changes of behavior in one context might alter behavior in other contexts.

The ability of a species to persist in fragmented habitats depends on both survival and reproduction within the remaining habitats, and movement between habitat fragments. It seems likely that fitness within habitat fragments depends on not just one type of behavior, but on an entire suite of behaviors (e.g. foraging, aggression, mating, parental care). Furthermore, both the tendency and ability to disperse should depend on a behavioral type (e.g. boldness: c.f. Fraser et al., 2001; aggressiveness: c.f. Chitty, 1960). Correlations among these behaviors could play an important role in explaining the relative ability of different species to cope with habitat loss, or more generally, to persist in metapopulations or source/sink populations. Besides, the presence of different personality types in populations will determine the ability of a species to persist in a degraded habitat. For example, bold individuals may be able to locate novel resources if the traditional resource fails, or aggressive individuals may be better at competing for resources as they become more limiting, thereby enabling local populations to persist under anthropogenic challenges (Sih et al., 2004a).

Studies in animal personality may contribute to identifying traits associated with the invasive behavior of some alien decapod species (see Hänfling et al., 2011 for a review of invasive crustaceans). The bold/aggressive/active behavioral syndrome, as analyzed at the species level (c.f. Mettke-Hofmann et al., 2002), may explain the success of a species in each of the four phases of the invasion process (transportation, release, establishment, and spread) as defined by Kolar and Lodge (2001): bold individuals disperse readily, aggressive

individuals compete well with native species, and aggressive/active individuals have major impacts on the invaded community. Besides, the dispersal process *per se* might select for bold/aggressive/active individuals (i.e. only these animals disperse), who then have a particularly strong tendency to disrupt the invaded communities. A recent study by Pintor et al. (2008) showed the existence of a positive correlation between aggression, activity and boldness in populations of the invasive signal crayfish *Pacifastacus leniusculus* in both native and invaded ranges in Oregon and California. The overall aggressive behavioral type of this crayfish species, as opposed to the non-aggressive, inactive and shy Shasta crayfish *Pacifastacus fortis*, might explain the success of the former (and the endangered status of Shasta crayfish) as the result of *P. leniusculus*' ability to both outcompete native crayfish in highly productive habitats and form established populations in low productive streams (Pintor et al., 2008).

Finally, it has been recognized that similarities in behavior between invertebrates and 'higher' animals should denote analogies in their cognitive experiences, including suffering (see the principle of argument-by-analogy; Sherwin, 2001). Following the way opened by Mather (2001) and Mather and Anderson (2007) for mollusk cephalopods, current research has started to make a case for sentience also in crustacean decapods (Elwood and Appel, 2009; Gherardi, 2009). As a result, the expected intensification of studies on personality in decapods will hopefully gather some needed evidence in support of the issue of welfare in this taxon.

Going back to Gosling and John's (1999) metaphor, we should admit that the here shown map of the 'personality continent' in decapods is far from being perfect: land masses are missing, boundaries are poorly defined, and theories such as plate tectonics have not yet been formulated. We are, however, confident that this vast underexplored area of investigation will soon provide many opportunities for exciting discoveries.

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