Chapter 10
Consider the Individual: Personality and Welfare in Invertebrates

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Abstract Personality, defined as consistent between-individual variation in clusters of behavioral traits independent of factors such as age or sex, emerges in most animal species tested so far. The number of invertebrate species discovered to have clear personality profiles is rapidly increasing. This previously neglected variation harbors many unsolved questions about its evolutionary maintenance and consequences, as well as about underlying proximate mechanisms, and it relates to the way individuals cope with stress behaviorally and physiologically. Importantly, it poses new challenges about welfare consequences, since the individuals emerge as the primary target of assessment and adjustment, and not the species. In fact, the effect of individual personalities on suitability for captivity and the efforts necessary to accommodate individuals of any given invertebrate species have not been considered, despite some anecdotal evidence from keepers, e.g., in octopuses, indicating its potential relevance. After an overview on what personality is and why this concept may be relevant to welfare, we enlist challenges and opportunities offered by invertebrates by presenting a series of case studies: cnidarian aggression, spider sexual cannibalism, cephalopod enrichment and escape, and colony personality in social insects. We conclude that because animals of many invertebrate phyla have distinct personalities, fine-tuning welfare provisions to what suits the individual best is recommended.

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10.1 Introduction

Hundreds of species of all taxa, but mostly vertebrates, have been shown to possess individual personalities (Carere and Eens 2005; Carere and Maestripieri 2013). This previously neglected variation is one of the most important recent foundations in behavioral biology, with the realization that it harbors unsolved questions about its evolutionary maintenance and consequences, as well as about underlying proximate mechanisms (Reale et al. 2007; Caramaschi et al. 2013; Koski 2014; Roche et al. 2016). Importantly, it poses new challenges about applied welfare consequences, since the individual emerges as the primary target of welfare assessment and adjustment, not the species. Since individual personality profoundly affects behavior and physiology, it thereby influences individual welfare, while welfare conditions could directly influence behavior, physiology, and personality (Fig. 4 in Finkemeier et al. 2018). Notably, individual needs (e.g., for compatible housing in social species and environmental enrichment) and individual lifetime experience are repeatedly recommended to be taken into account in the Directive 2010/63/EU.

First, this is an intersection of two poorly studied and often neglected topics. We do not know much about the personality of invertebrates (see Mather and Logue 2013; Jandt et al. 2014; Kralj-Fišer and Schuett 2014, for reviews). Second, information about what welfare of invertebrates might consist of is thin. In fact, the effect of individual personality on suitability for captivity and the efforts necessary to accommodate individuals of any given invertebrate species have not been considered.

Until quite recently the variation of behavior among individuals of any animal species was overlooked. Consistent behavioral differences (behavioral syndromes or personalities) were denied, especially for animals other than mammals and birds. Research has begun to change that, as testified by Carere and Maestripieri's (2013) book and Gosling's (2001) explicit linkage of animal personality studies to human research. However, invertebrates are often ignored (Horvath et al. 2013). Kralj-Fišer and Schuett (2014) report finding nearly 4000 references to vertebrate personalities in December of 2013. In contrast, Mather and Logue (2013), with data extracted several years previously, found studies in only 19 invertebrate genera, 15 within the Arthropoda. Kralj-Fišer and Schuett (2014) report an increase in studies of personalities of invertebrates, with 243 publications, only 47 of which were empirical studies. Again, most were in the Arthropoda, though this is the most numerous phylum in the animal kingdom, yet the contrast in focus between the invertebrates with 34 phyla and the single subphylum Vertebrata is clear. Very recently the tendency to study personality in invertebrates has further increased (e.g., Cronin 2015; Carere et al. 2015a; Planas-Sitjà et al. 2015; Blight et al. 2016; Santostefano et al. 2016; Udino et al. 2017), in parallel with studies on their cognitive abilities and sentience (especially in social insects) that are significantly boosting the general attention to their welfare (e.g., Barron and Klein 2016; Perry et al. 2016; d'Ettorre et al. 2017; Baracchi et al. 2017).

It is therefore clear that the welfare of invertebrates has received little and only recent attention. One reason for this is that we tend to care about animals similar to us, and invertebrates simply appear very different (see Boppré and Vane-Wright 2019); empathy is easier if one can consider behavioral similarities (Kellert 1993). Invertebrates were considered "things," not animals, and the discussion as to whether "lower" animals can even experience pain and suffering has not receded; note Key (2016) and the recent debate of whether fish feel pain as well as the recent similar debate on crustaceans (Elwood and Adams 2015; Elwood 2016; Stevens et al. 2016). Even with the 3R (refine, reduce, replace) animal welfare approach, one of the tenets is "replace" (Horvath et al. 2013), and this was sometimes considered to be replacement of "higher" vertebrates with "lower" invertebrates. Another factor that led to lack of consideration of the welfare of invertebrates was linked to the underestimation of their behavioral complexity and flexibility. Putting an animal in a simple learning situation in controlled conditions gave simple responses. Animals such as *Aplysia* gastropods have been used as a simple model for learning, but when they are given variety and choices, we are finding that invertebrates' behavior is not at all simple. This was suggested long ago by Leonard and Lukowiak (1986) for this species but has been emphasized much more widely by Brembs (2013) for neurophysiological testing, in evaluation of natural behavior, and when animals are given situations with choices. Research on cognition is spreading from the vertebrates to social insects, cephalopods, crustaceans, and spiders (e.g., Bateson et al. 2011; Loukola et al. 2016; Perry et al. 2016; Alem et al. 2016; Desmedt et al. 2017; Udino et al. 2017; Marini et al. 2017; Wolff et al. 2017). De Waal (2016) has commented that scientists' finding that one animal or group has some cognitive ability stimulates others to find it in quite different species.

A pressure, which has brought gradually to increase consideration of individuality in invertebrates, is the ethical changes that have spread over the last 50 years. Gluck (2016) describes how 50 years ago animals, even vertebrates, were units or numbers, and the psychological testing did not admit them to be actual living beings. Early in her career, Jane Goodall was discouraged from giving her chimpanzees names because that was "too subjective." The Cartesian value, that animals were no better than machines, was the dominant ethos (Mather and Anderson 2007). This was gradually replaced by a utilitarian ethic, one that is often still prevalent, of relative value and gains and losses. This is evident as many advocates of invertebrate research suggest it would advance our knowledge for human well-being or benefit us by providing food or behavioral models (Horvath et al. 2013; Kralj-Fišer and Schuett 2014; Vitale and Pollo 2019). It is mainly the Animal Rights approach (Regan 2001) that focused on the individual and its welfare. Regan believed that we should look at what is good for the individual animals and asked to ensure them a full and complete life. That is what this book and particularly this chapter will ask: how could we use that viewpoint?

Cooke et al. (2019) point out that there are several settings in which we control the lives of invertebrates, and that the issues and possibilities are different for each. Animals used for research are tightly controlled so that only experimental variables can be manipulated, and this may lead to unrealistic restrictions (see van Akker et al. 1994, for the use of chimpanzees in AIDS research). Animals that are raised in culture for food or other human ends may be similarly restricted—for instance, cephalopods would not be allowed to reproduce as this results in the end of their life. But the utilitarian approach also puts pressure on animal keepers for better welfare, because animals that are better kept for human consumption are often thought to taste better or in general to be of higher quality. There is now a huge industry in animal display, in zoos, aquariums, and zoological parks. Here there is public pressure toward animal welfare, though also pressure to manipulate animals to groups and situations that "seem right." The Disney film 'Finding Nemo" featured a family-like setting and ignored the fact that anemone fish are protandrous hermaphrodites (Cooney 2013). Hobbyist keepers of individual pets, of course, have a huge investment in good welfare for their animals, although they are often ignorant about their needs and benefit from education, as well as being very anthropocentric about animals' lives.

Given these pressures, what kind of decisions can keepers make about individual invertebrates in their care? One is surely to select particular individuals in the first place. Anderson (1984) wrote about the selection of giant Pacific octopuses for the Seattle Aquarium based on personality, and one particularly shy individual nicknamed Emily Dickinson was hopeless as a display animal. A similar constraint would be on when to keep individual animals—are they allowed their full lifespan, including reproduction or other key life events so that animals can express what Regan (2001) calls a full, rich life (Anderson 2000)? A second kind of decision, possibly the most important, is to decide how to construct or alter their environment when they are in captivity and how to find the individual's behavioral capacity and make sure it can exercise it (and see Cooke et al. 2019 for a discussion of this). Finally, of course education of all individuals concerned builds a better future.

Personalities are clusters of behaviors that are repeatable across time and/or contexts, at the level of the individual (Reale and Dingemanse 2012). Over the past two decades, there has been an explosion of research on this topic in animals belonging to diverse taxa ranging from invertebrates (especially cephalopods, social insects, crustaceans, and spiders; for the former see Table 10.1), fish, birds, and mammals (Carere and Maestripieri 2013). This body of work shows within-species interindividual repeatability in typically studied personality traits: aggression, boldness, activity, exploration, and sociability (Reale et al. 2007; Bell et al. 2009; Carere et al. 2010; Roche et al. 2016). Research on invertebrates so far has highlighted similar personality dimensions, but, as highlighted by Kralj-Fišer and Schuett (2014), such an approach is needed because of the life history aspects that are often rare or absent in vertebrates, thereby offering new research perspectives. One could think, for example, about eusociality, complete metamorphosis, or asexual reproduction and the possibility to tackle, respectively, questions like individuality versus collectivity, (in)consistency across metamorphosis, or gene-environment interactions in genetically identical individuals. A common sense notion is that invertebrates are somehow more "rigid" than vertebrates in their behavior, with little interindividual differences. However, no significant differences were found in repeatability of behavior of invertebrates and vertebrates in the meta-analysis conducted by Bell et al. (2009), while the "stereotyped" hunting sequence of the

Table 10.1 Cephalopod studies assessing consistent behavioral differences over time, situations, and/or contexts

Species	Common name	Behavioral trait(s)	Time consistency tested	Evidence time/situation consistency	Context consistency/BS tested	Reference
Octopus rubescens	Red octopus	Threat response, feeding	Yes, short term	Partly	Yes (among tests)	Mather and Anderson (1993)
Octopus vulgaris	Common octopus	Threat response, feeding	Yes, short term	Partly	Yes (among tests)	Pacchiarotti (2018)
Euprymna tasmanica	Dumpling squid	Threat response, feeding	Yes	Yes	Yes (among tests)	Sinn and Moltschaniwskyji (2005)
Euprymna tasmanica	Dumpling squid	Threat response, feeding	Yes	Yes	Yes (among tests)	Sinn et al. (2008)
Octopus tetricus	Gloomy octopus	Response to conspecific video	Yes	Episodic	Yes (among tests)	Pronk et al. (2010)
Sepia officinalis	Cuttlefish	Threat response, feeding	Yes, short term	Partly	Yes (among tests)	Carere et al. (2015a)
Sepia officinalis	Cuttlefish	Threat response, hunting sequence, hunting ability	Yes, short term	Yes	Yes (among tests)	Zoratto et al. (2018)

Among tests: correlations conducted between variables measured in different tests; BS tested: correlations between behaviors tested (behavioral syndrome). Modified from Kralj-Fišer and Schuett (2014) cuttlefish harbors an interesting and meaningful variation across adult individuals, which relates to personality differences (Zoratto et al. 2018).

Another avenue of research suggests that personality should be taken into consideration when evaluating the welfare of animals, since personality types are differently linked to affective states. For instance, some personality types are likely to score more pessimistic than others in cognitive bias tests (honey bees, Bateson et al. 2011; carpenter ants, d'Ettorre et al. 2017). Invertebrates are widely used in animal experimentation as well as in zoos and aquaria, and there is a growing interest and concern about their welfare upon realizing that many species possess advanced cognitive abilities, consciousness, individuality, pain suffering ability, etc. (Carere et al. 2011; Horvath et al. 2013). An important tenet of research in animal personality (including humans) is that different personalities typically have a differential vulnerability to stress and thereby also a different susceptibility to disease (coping styles, Koolhaas et al. 2001; Carere et al. 2010). Such aspects directly relate to welfare, and although invertebrate studies in this respect are indeed scanty, their stress response is similar to vertebrates in many respects (Stefano et al. 2002; Adamo 2012, see also Elwood 2019). So it can be argued that similar personality-related differences in coping with stress as in vertebrates could be found in invertebrates.

Finally personality could have significant welfare-related implications in captive breeding and restocking/reintroduction projects, either because of methodological issues (sampling bias of bold individuals in capture-recapture studies) or because of the (in)adequate behavioral profiles assessed when animals have to be released in the wild (Gherardi et al. 2012; Carere et al. 2015b).

By presenting four cases where—we believe—personality matters for welfare, we would like to extrapolate relevant issues, questions, and challenges that need to be pursued with the perspective offered by invertebrates.

10.2 Case I: Cnidarian Sea Anemones and Aggression

Sea anemones are in the phylum Cnidaria, and they look so much like marine flowers that even people who know they are animals have difficulty remembering that they are not. Although they have a diffuse nervous system with no central control, they are predators. They are equipped with stinging nematocysts that are deadly to some animals and uncomfortable to humans. Depending on the species, they are somewhat mobile, as they can detach their pedal disc from the substrate and move to a new location. They have feeding tentacles, which initiate contact with potential prey and other items. Some anemones such as *Actinia* also have specialized tentacles called acrorhagi containing nematocysts, which damage conspecifics and potential prey, and anemones have conflicts (Rudin and Briffa 2011). Anemones that come in contact with one another begin with assessment by the feeding tentacles, and often the smaller individual moves away, and the contest simply resolves as withdrawal. But in some cases, they advance their acrorhagi and begin to sting one another, and the one that receives the most damage from the stings then withdraws. When related individuals fight, the damage is greater (Foster and Briffa 2014).

What does this have to do with personality? Individuals vary in response to a puff of water aimed as a startle test, and a shorter latency to re-extend the feeding tentacles after startle indicates boldness, a highly repeatable characteristic (Briffa and Greenaway 2011). Winners of fights show less startle, and the difference is greater after fights (Rudin and Briffa 2012), so they have both simple personality and plasticity. *Condylactis* anemones, sometimes called purple-tipped, are more mobile and common in shallow water, often living in crevices or moving slowly by detaching and attaching the pedal disc (Zahra 2017). They also have difference along the shy-bold continuum when given the startle test, and they vary in habitat choice and number of nearby conspecifics, depending on personality (Hensley et al. 2012).

There are obvious welfare concerns when keeping more than one anemone, and even the most liberal animal welfare regulations do not cover Cnidarians. If animals fight and inflict damage on one another, it would be ethical to prevent this, although anemones "make a good showing" on display in professional aquariums when they are presented in groups for a greater visual effect. Equally, if we could predict how to select non-aggressive anemones for display, we should do so. Given that we do not know how to select against aggressive anemones, we could alter the environment with a couple of physical design features that would obviously assist the anemones in avoiding damaging fights. First, if they are dispersed in a tank or given the opportunity to disperse, fights would be reduced. Second, if anemones choose different habitats partly dependent on their personality, then a tank should contain a variety of habitat that anemones could select. There are likely species or strains, which have fewer damaging fights, but the personality of the individuals also has to be taken into account.

There is a different problem for hobbyists keeping pets in home aquariums. Anemones are colorful animals and attractive components of a home aquarium. A general guide to keeping them (Barrington 2018) comments that anemones are difficult to keep and that they need good water quality, high levels of dissolved oxygen, a stable salinity, and some water flow, as well as lighting appropriate for keeping their algae healthy. Fortunately, hobbyists probably do not think in terms of multiple individuals, as she talks of "your anemone." But there is nowhere a suggestion that anemones might be harmful to each other and that their welfare might have social as well as physical concerns. This aspect of keeping anemones obviously needs a clear education effort to assure the animals' welfare.

10.3 Case II: Spiders and Sexual Cannibalism

The theoretical basis for the research on female spiders that kill prospective or actual mates is a bit different than that of personality research. It is based on the idea of behavioral syndromes, which are correlations of differences in individuals through time and across situations (Sih et al. 2004; Bell 2007). Syndromes are a property of populations rather than characteristics of individuals. They are firmly based in ecology, in that they expect that natural selection favors different optima in different situations. Thus a tendency like aggression or shyness that is optimal for one context or life event might not be optimal for another and yet would persist. The benefit of this viewpoint is its emphasis on carryover, and its drawback is that it may focus too closely on one dimension when actually a suite of them is inherited together. However, the behavioral syndrome approach offers a logical explanation for situations where a trait does not seem to be adaptive. One of these situations is sexual cannibalism, especially as studied in female spiders to their prospective mates. This is a welfare issue too, as death and its avoidance is central to biology (Maderspacher 2016), but those who keep animals in captivity do not usually intend their death.

The problem of sexual cannibalism was raised first in desert spiders both in terms of their adaptive behavior to different habitats and the foraging tactics of different individuals (Pruitt and Riechert 2012). Several behaviors were studied—prey breadth, attack latency, excessive killing, antipredator boldness and sexual cannibalism—in these spiders, and there were clear correlations. Johnson and Sih (2007) found that fishing spiders that live on the water's edge also have a carryover between boldness in predator threat and as adults, including in mating. The fact that cannibalism occurred especially in spiders that were eager also to attack prey, seen also in comb-footed spiders, led them to suggest that an "overflow" of aggression might lead to sexual cannibalism. Pruitt and Reichert (2009) suggested a trade-off in fitness for these species of spiders and found a correlation between aggression with conspecifics, eagerness in foraging, and precopulatory cannibalism. Foellemer and Khadka (2013) also saw that orb web spiders that were "aggressive" foragers were more likely to attack mates, so this began to look like a general pattern across the solitary spiders.

Of course, this produces a dilemma for scientist who keep spiders to study them and institutions that might want to display them. The researcher with a limited supply of animals that she/he wants to keep must also be sensitive to the supply of the next generation, and if the best way to get more offspring is to sacrifice some of the present one, that is a dilemma. The institution that displays them also faces a dilemma: is it reasonable to display the whole lifespan of a species, remembering the Regan (2001) concept of giving animals a full, rich life, when it results in the death of some of the members? Western society is death-avoiding (Kellehear 1984) and choosing aggressive female spiders that kill their mates is not easy to show. There is always a public outcry at sacrificing any captive animal (see Levin 2015, for Marius the giraffe). But how to tell whether an individual spider should be chosen because she doesn't eat well and won't eat her mate?

More detailed work should make sure this is really the case. If sexual cannibalism the inevitable outcome of voracity, do we have to select spiders that feed well or those that won't kill their mates? With detailed research in lab and field, the results are mixed. With the orb web spider, Foellemer and Khadka (2013) found that there is a correlation between aggressive foraging and attack on mates with the insertion of one of two pedipalps but suggest an alternative possibility, that it has evolved to allow a female more mate choice. Lichtenstein et al. (2016), looking for a relationship with hunger, find that web-building spiders only show these differences clearly when food is readily available. On the other hand, Johnson (2001) found that 20% of fishing spiders remained unmated, but this was not due to cannibalism. While cannibalizing females were more likely to have a hatch of eggs, they were also larger, so this could explain the outcome. Andrade (1998) studied male redback spiders in lab and field. Even though males put themselves in front of females in "sacrifice," only around 50% of females actually killed and ate them, and that choice depended on female hunger levels. Kralj-Fišer et al. (2013) suggested instead that there might be assortative mating in that aggressive females accepted aggressive males. They rejected the aggressive spillover hypothesis for sexual cannibalism (Kralj-Fišer et al. 2012), instead suggesting that *Nephilengys* spiders did show boldness in attacking prey and avoiding predators but that their sexual cannibals were not more likely to attack a prospective mate; rather they attacked the less aggressive suitors.

Clearly there are differences depending on the species and the conditions, but the overflow hypothesis is not universally supported, and the trade-off between keeping a spider that will feed well and be ready to produce eggs and keeping one that will attack mates is not absolute. Researchers can alter the environment to generate the conditions that will avoid cannibalism and yet select aggressive females so that they can keep the next generation. Those who want to display the full life cycle of spiders and who want to carry out Regan's (2001) emphasis on animals living a "full, rich life" do not have to choose between their animals' safety and their survival. Bold spiders may be more likely to attack their mates, but provision of sufficient food (Andrade 1998) and males also of sufficient quality (Kralj-Fišer et al. 2012) can avoid the likelihood of demonstrating the death of one of the protagonists, though there is obviously no guarantee.

10.4 Case III: Octopus Enrichment and Escape

Octopuses are arguably the most obvious case for invertebrate welfare. They have big brains and manipulative arms, and they also explore, play, and have the capacity for many forms of learning (Mather 2008). In addition, they have clear personalities (Mather and Anderson 1993), along three dimensions of activity, reactivity, and avoidance, and the conditions that are right for one octopus to thrive are not necessarily the ones that will suit another. Given the opportunity to play with an object, a floating pill bottle, only two of eight individuals did so. While we do not understand the cognitive capacity of animals in other phyla, keepers of octopuses generally believe that they can become bored, and see Anderson and Wood (2001) and Cooke et al. (2019) for techniques to keep them occupied. From a utilitarian approach that might be necessary if one cultured them, people find that octopuses given an enriched environment do better and gain weight (Beigel and Boal 2006). Given a sterile environment, octopuses can also escape. As they are also the subject of animal welfare regulations (see Ponte et al. 2019), octopuses need special consideration, and one of the necessities is to find out what works for the individual octopus, not just the group or even the species.

For professional aquariums which display octopuses, individual differences are a big problem, and Anderson (1984) writes of the criteria for the large *Enteroctopus dofleini* that make an octopus suitable to select for display. A shy animal, one that stays in hiding nearly all the time, is not visible and needs to be released into the wild and replaced. An active animal is best for public viewing, but active animals are also exploratory and may escape or damage their tank. He writes of one octopus that clipped off the wires holding the plastic pan under the gravel substrate, dug it up, and tore it into pieces, leaving them floating on the surface of the water in the tank. Other octopuses may be more reactive and shoot jets of water at their keepers, not damaging but disconcerting. On the other hand, Montgomery (2016) writes of her encounters with an octopus that could only be called "friendly" which gave her and others a rich experience with another animal's reality. Still, other octopuses have been known to grasp the hand of keepers when they are feeding or cleaning the tank and pull strongly enough to leave suction marks all along their arms, and this might be a concern for human welfare. If you can do so, selection of appropriate octopuses is advisable.

Individual difference in feeding may also be a problem for hobbyists who want to keep their pet octopuses in good condition. Octopuses can be considered to be specializing generalists (Anderson et al. 2008). They are predators, mainly of crustaceans and molluscs, and prefer prey that is alive and moving. They can be taught to take thawed frozen prey such as shrimp or even pieces of squid, but this is not preferred, and an octopus that is really a specialist may not adapt to this kind of food. On the other hand, a generalist animal may accept such items as pieces of chicken or even eggs, adding variety to the diet and pleasure to watchers (Anderson 2008). Since octopuses are manipulative, both professionals and amateurs have provided them with "puzzle boxes" enclosing food so that they have the opportunity to work at attaining the food, also enhancing their display. Cooke et al. (2019) point out that such enrichment will continue to be a problem until we understand the animal better, as what is enriching for one individual may be threatening for another.

By far the biggest problem for anyone keeping an octopus is their tendency to escape. Octopuses have no bones, rather move by jet propulsion or by the muscular hydrostat movement system in their eight arms (Kier and Smith 1985). As the arms are also lined with suckers, they can exert considerable force (Dilly et al. 1964), and octopuses can also compress their body to a very small diameter. An active octopus that perhaps is bored will be able to escape even well-crafted enclosures, and individuals over the years have gained considerable notoriety by doing so—except that they may end up dead on the floor. Wood and Anderson (2004) have evaluated the tendency of different species to escape, and perhaps it is good advice for a hobbyist to choose to select a species as a pet with fewer escaping tendencies. Again an active octopus is more interesting to view on display, but both the loss of an expensive animal and the concern of animal's welfare committees (see Ponte et al. 2019), who take a dim view of an animal's loss, counter this advantage. Altering the physical environment is the best response, and until we understand the individual better, overreaction is the only route to confining an octopus (see Wood in Mather et al. 2013). Heavy weights on top of the tank lid (bricks are often used) can decrease the likelihood that an octopus can escape by that route; locking lids are a good solution if they can be crafted. Accessory areas such as filtration chamber provide escape routes, and they should be as blocked off as well as possible, keeping in mind that the octopus' pulling power is formidable as well.

10.5 Case IV: Colony and Individual Personality in Social Invertebrates

While most solitary animals have obvious variation in personality, the situation is more difficult in social animals. Jandt et al. (2014) point out that there are several levels of variation for social insect populations. There is within-colony variation in morphological castes that are specialized for such behavior as foraging, brood attention, and aggression but also non-morphological behavioral variation, as well as variation in task selection across time (temporal polyethism). These can lead to colony-level variation, which can correlate with the success of the whole colony, and one interesting area of investigation is which individuals are influencing the collective most. Influenced by the behavioral syndromes approach (Bell 2007), several authors have looked for trade-offs due to the influence of one tendency in several situations, and of course for culture of social invertebrates, this success is the "bottom line." Authors have looked, too, at social spiders, ants, and bees, and the conclusions for one of these groups might not hold for others.

Why does individual personality of members of a social colony matter to our interest and investment in one? Many authors have looked at productivity of the group, broadly conceived. Muller and Chittka (2008) point out that a mixture of personalities in bee foragers might match them to a varying environment, with slow accurate ones being better at finding food in different situations than fast sloppy individuals. Wray et al. (2011) found that bee colonies' variation was predicted by two factors, and these influenced both productivity of young and weight of the comb and also ultimately survival of the colony. Scharf et al. (2012) did a factor analysis of ant colony personalities and found that one factor, predicted mostly by nest reconstruction, influenced their productivity. Ant colonies were also influenced by a trade-off due to their position on the shy-bold axis. Boldness led to more exploration, aggression, and food supply but also to higher mortality because ants foraged in dangerous situations such as too high temperatures.

Pinter-Wollman (2012) asked what major factors might facilitate the influence of individual personality on colony personality and suggested that it might be the average personality of the group, external environment factors, or some influence of environment and gave strategies for finding answers. For this, Jandt et al. (2014) advanced the trade-off behavioral syndromes approach. Aggression across situations of feeding and reproduction has been stressed in solitary animals; see the section on spiders. Scharf et al. (2012) found that those ant colonies that showed low aggression failed to remove dead members and moved to new locations, although what mattered to productivity in the protected lab was nest reconstruction. Blight et al. (2016) pointed out that ant colonies differ in what might be called boldness and that more aggression does lead to more food for the colony and better defense but also to more mortality from this same tendency. This emphasis on particular measures or factors may depend as much on the approach of the researcher as the tendencies of the animals. Wray et al. (2011) studied collective colony personalities of bees and found that factors included "runniness," defense, foraging behavior, and lack of honey comb repair, but only the second and third factors predicted survival over the winter, critical to bee keeper cultivators. Similarly, Walton and Toth (2016) found that worker bees tended to divide into those doing more or less interactive tasks and that trophallaxis (food exchange) might be an important behavior. They also found that being part of the queen retinue loaded separately from the other supportive behaviors and components of nest maintenance were important but poorly understood. This paper reminds us to use an ethological approach and keep the basic behavior of the species in mind and also that bees, ants, and spiders might be quite different from one another.

Pinter-Wollman's (2012) question of the sources of colony personality has not been conclusively answered. Carere et al. (2018) found that ants grouped by personality emphasized the similarities and generated similar collectives, which suggests the first influence. However, Modlmeier et al. (2014b) emphasize the concept of the "keystone" individual, across many types of social group (see Sih and Watters 2005, for its origin), which would be the second. Such an individual or small group would not be one playing a social role but a distinct personality that was not replaceable. They might either enhance group performance or totally disrupt it. One example is in social spiders (Pruitt et al. 2013), where a few bold individuals may influence a colony to be much bolder than the average would be. Another example is found in honey bees, where 5% of colony individuals influence the whole swarm to lift off and move to a new location (Dornhaus et al. 2008). The external environment of habitat structure does influence the colony-level personality in some social spiders (Modlmeier et al. 2014a), so the third influence also matters. Clearly there will be no simple answers to such a fundamental question across such diverse groups.

Yet the possibility of a few keystone individuals changing the behavior of a whole group raises interesting questions and gives us a chance to think of opportunities for interventions in situations of cultivation. If aggression is the result of a few colony members, perhaps we can use selection by member removal so a social spider group can be made more docile and be more suitable for display. If a few bees cause the whole group to relocate and it's not a favorable time, perhaps their removal can change the timing. If different habitats can cause different spider personalities, alteration of the physical environment can make them more suitable for a zoo or insectarium public display setting. Research in this area is recent, the field is quite dynamic, and the combination of personality variation in groups and individuals is complex, but advances will no doubt help those who want to influence animal personality in these groups.

10.6 Conclusion

Ironically, while this book asks readers to evaluate animal welfare much more widely, this chapter does the opposite. We have made the case for broad evaluation of welfare of all animals, not just the vertebrates commonly considered. Yet conversely, the exact requirement for welfare may differ according to the individual. Some considerations of welfare, such as provision of social experience or housing, will depend on the phylum, class, or species. Because animals of many invertebrate phyla have distinct personalities, we argue here also for fine-tuning welfare provisions to what suits the individual best.

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