INVITED PERSPECTIVE

Why Do Some Fish Fight More than Others?*

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ABSTRACT

Reversible changes in how readily animals fight can be explained in terms of adaptive responses to differences in the costs and benefits of fighting. In contrast, long-term differences in aggressiveness raise a number of questions, including why animals are consistent with respect to this trait, why aggressiveness is often linked to general risk taking, and why aggressive and nonaggressive animals often coexist within a population. In fish, different levels of aggressiveness bring several direct fitness-related consequences, such as when aggressive individuals monopolize a limited food supply and grow fast. They also bring indirect consequences, such as when aggressive fish are more susceptible to predation and when they require a larger respiratory surface to service a higher metabolic rate. Fitness consequences of aggressiveness are often context dependent, with aggressive fish tending to do well in simple, predictable conditions but not in complex, less predictable conditions. The diverse, context-dependent consequences of aggression mean that aggressive and nonaggressive fish flourish in different conditions and explain in general terms why these behavioral phenotypes often coexist. There are a number of candidate evolutionary frameworks for explaining why individual differences in aggressiveness are often, but not always, consistent over time and often, but not always, linked to differences in general risk taking.

Variable Aggressiveness among Fishes

Aggression, sometimes defined as behavior that actually or potentially causes harm to another animal of the same species, is a conspicuous feature of the behavior of many kinds of fish. In contrast to scramble competition, where all animals have access to a resource and each individual gathers as much as possible, during aggression or interference competition, rivals are actively excluded from access to resources. While aggression of some sort is widespread, there is considerable variation between fish species in how readily members fight; for example, mobile, pelagic fish do not fight much, whereas in spatially restricted benthic species, such as many coral reef fish, aggression is common. Within a given species, the tendency to fight may vary between populations and according to gender, with males being more aggressive than females in many species. It also varies in relation to developmental stage, for example, when salmonids switch from aggressive, territorial behavior to nonaggressive schooling at smolting. In addition, even among individuals of the same species, population, gender, age group, and size, some fish fight more than others; this is not noise but important biological variability that it is necessary to recognize and explain. A general review documenting such variability in fishes can be found in Damsgaard and Huntingford (2012). In this article, we discuss differences in individual aggressiveness in fish, providing examples and then considering their consequences for fitness. For reasons of space, we have chosen not to address the equally important questions of how such differences develop and the roles of genetic and environmental influences in this process.

Figure 1 gives two examples of variability in levels of aggression shown by age-matched individuals of two species of teleost fish, juvenile Atlantic salmon (*Salmo salar*) and adult goldfish (*Carassius auratus*), held in small groups (Adams et al. 1998; Tamilselvan 2010). Within groups of salmon, there are clearly one or two fish that are frequently observed attacking their companions and others that rarely show this behavior. Compared to many salmonids, goldfish are generally regarded as nonaggressive. However, here, too, while the majority of fish within a group show little if any aggression, there are a number of individuals that attack at a reasonably high rate. Where such differences in aggressiveness occur, these could be the result either of reversible differences in behavioral state or of long-lasting, consistent individual differences.

Temporary, Reversible Changes in Responsiveness

Figure 2 shows an example of variable aggression arising from reversible differences in behavioral state. Individual breeding male three-spined sticklebacks (*Gasterosteus aculeatus*) show
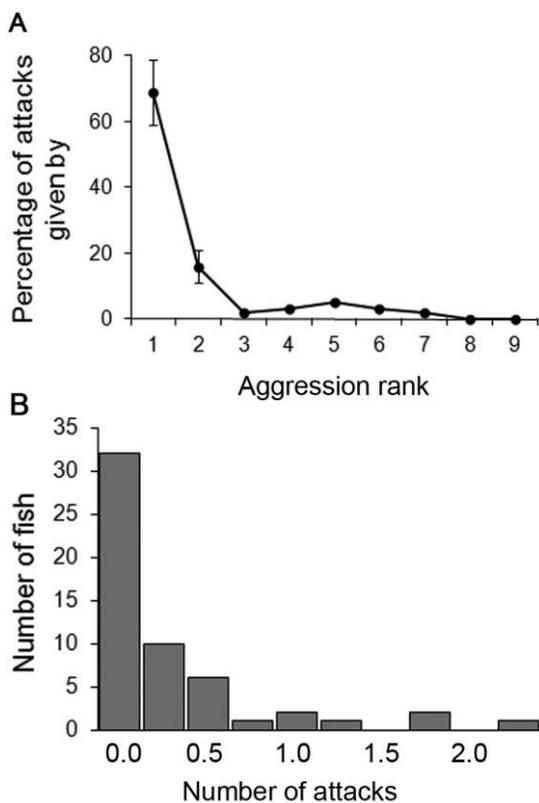
Figure 1. A, Mean (±SE) percentage of all observed attacks given by individual juvenile Atlantic salmon held in small groups. Numbers on X-axis refer to the aggressive rank given to each individual based on the number of attacks it performed (Adams et al. 1998). B, Frequency distribution of the number of attacks delivered per minute of observation by individual goldfish held in small groups (Tamilselvan 2010).

less aggression toward a standard opponent (another breeding male confined in a glass flask) when the encounter takes place in the presence of a perceived threat from a predator and when their nests are empty than in the converse conditions (Ukegbu and Huntingford 1988). Behavioral ecologists explain such reversible shifts in response to a rival in terms of a balance between the costs and benefits of fighting. On the positive side, aggression can result in fitness-related benefits to the victor in terms of preferential access to resources. For example, in juvenile Atlantic salmon, the two most aggressive fish within a group between them gain nearly 50% of all delivered food (fig. 3A; Adams et al. 1998). In goldfish, fish that show no aggression may gain access to a spatially restricted food but may also be unsuccessful at feeding; in contrast, fish that show more than one bite per minute always manage to feed. In other words, the benefit of aggressive behavior in this context is reliable access to food (fig. 3B; Tamilselvan 2010).

Balanced against such benefits, taking part in a fight, particularly if this is unsuccessful, has negative effects on the animal involved; in other words, it imposes costs. In the first place, fights are energetically expensive; for example, when male cichlid fish (Aequidens rivulatus) fight over breeding territories,

respiration rate increases as encounters progress in both participants, but particularly in the loser (Maan et al. 2001). In the same context, in male Tilapia zillii lactate accumulates and glycogen reserves are depleted as fights progress, in both participants, but again particularly in the loser (Neat et al. 1998). Such physiological costs of fighting are mediated by a variety of endocrinological changes, which may in themselves be costly to generate (Briffa and Sneddon 2007). A second potential cost of aggression is that taking part in a fight may result in injury, even in fish, which tend not to have specialized weapons. For example, by the end a fight between breeding male T. zillii, both participants can have missing scales, but this is more marked in the loser than in the winner (median no. lost scales = 5 for the winner and 7.5 for the loser; Neat et al. 1998). The studies mentioned above were all carried out in the laboratory, and it is worth noting that costs may differ in fish fighting in the wild (Sloman and Armstrong 2002).

How much a given fish fights in a given context depends on the balance between the benefits of winning and the outcome-dependent costs of taking part in fights. For example, in the case of the male sticklebacks shown in figure 2, the increase in aggressiveness in fish with eggs in their nest, regardless of whether a predator is present, reflects the greater value of a nest full of eggs compared to an empty nest and thus the increased fitness benefits of protecting it successfully. The drop in aggression in the presence of a predator, regardless of nest status, reflects increased costs of fighting because fish engaging in fights are both more conspicuous and less vigilant (Jakobssen et al. 1995). It is well established that the probability that a fish will win a contest against a given opponent depends on its relative size, past experience of winning and losing, and its period of residence in a disputed area. In the present context, these effects modulate the likely costs and benefits of fighting (for reviews, see Briffa and Sneddon 2007; Damsgaard and
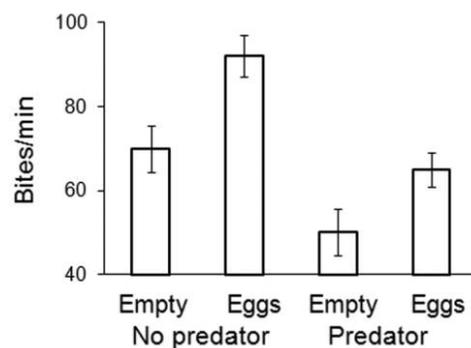
Figure 2. Mean (±SE) number of bites delivered per minute toward a standard opponent (a breeding male conspecific confined in a glass flask) by individually housed breeding male three-spined sticklebacks either with ("Eggs") or without ("Empty") a clutch of eggs in their nest, in the absence of predation risk ("No predator") and when in visual contact with a potential predator (a brown trout behind glass; "Predator"). The same 29 fish were tested in all four conditions (Ukegbu and Huntingford 1988).
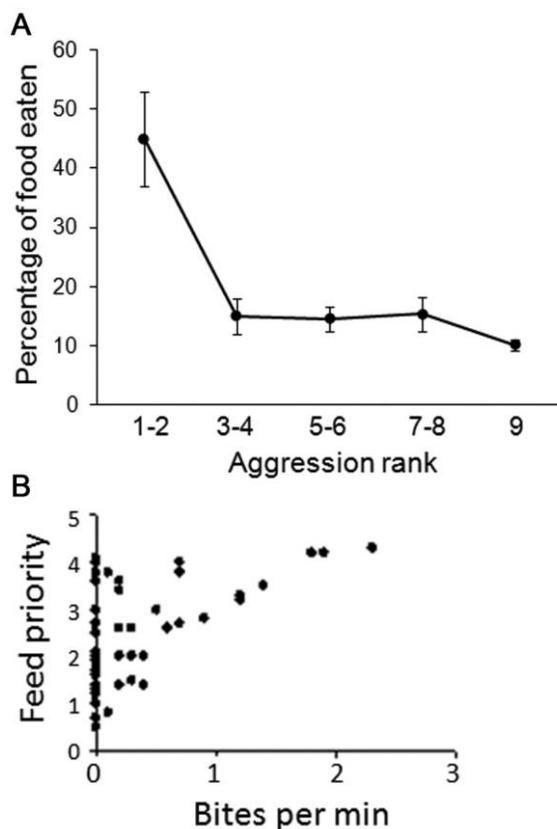
Figure 3. *A*, Percentage of food eaten by individual juvenile Atlantic salmon held in small groups in relation to rank assigned according to frequency of expressed aggression (combined over pairs of adjacent rank; Adams et al. 1998). *B*, Effectiveness at competing for access to spatially restricted food (feed priority, measured as the proportion of food items potentially available to a given fish that it acquired and ate) in individual goldfish held in small groups, in relation to the number of bites observed per minute by a given fish outside the feeding periods (averaged across observations; Tamilselvan 2010).

Huntingford 2012). Where animals show short-term reversible differences in aggressiveness, drawing on decision-making mechanisms that are themselves the product of natural selection, functional explanations of variability (referring to its implications for fitness) clearly exist in terms of the opposing costs and benefits of fighting.

Consistent Individual Differences in Aggressiveness and Correlated Traits

In many species, some individuals are consistently more aggressive than others of the same species, population, gender, age, and size held under identical conditions. Such differences can be detected beneath the temporary, reversible changes that occur as animals unconsciously adjust their aggressiveness to the costs of fighting and the benefits of victory. Again, the three-spined stickleback provides a good example; figure 4*A* shows the scores for the same individual male stickleback tested for aggressiveness toward a standard opponent on two occasions

separated by an interval of at least 1 wk. The strong positive relationship between the two scores indicates consistent individual differences at least on this timescale (F. Huntingford, unpublished data). Thus, how fiercely a male stickleback defends its breeding territory on one occasion predicts what it will do on another. It also predicts how the fish will behave in the face of other challenges. Figure 4*B* shows the relationship between aggressiveness of individual fish during the breeding season and a measure of risk taking (readiness to explore a novel, potentially dangerous environment) by the same fish several months previously, well before the breeding season. Here, too, there is a significant positive relationship. Those individuals that take risks when confronted by a predator are particularly aggressive during the breeding season; those that
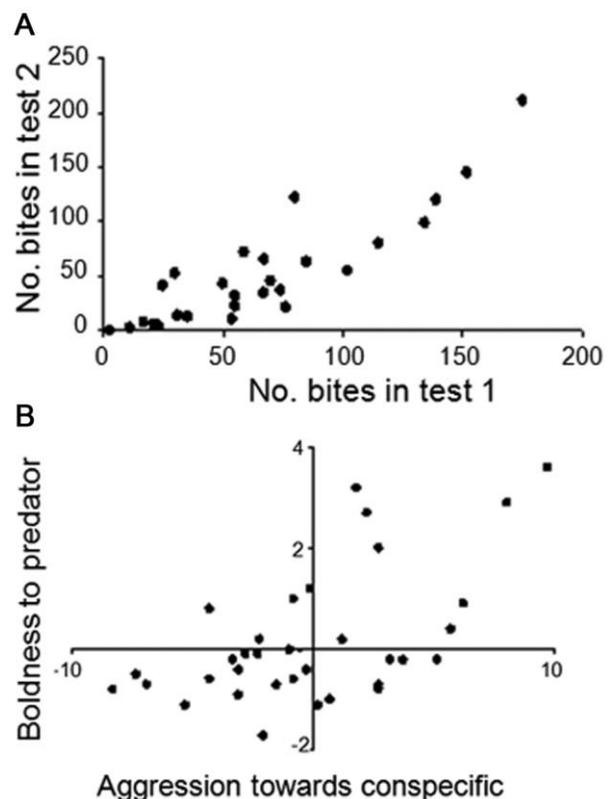
Figure 4. *A*, Number of bites delivered by individually housed breeding male three-spined sticklebacks toward a standard opponent (a breeding male conspecific confined in a glass flask) during two 5-min tests (test 1 and test 2) carried out with an interval of at least 7 d; $R^2 = 0.75$ (F. Huntingford, unpublished data). *B*, A multivariate measure of risk taking (boldness) in the presence of a potential predator in individual male three-spined sticklebacks tested outside the breeding season in relation to a multivariate measure of aggressiveness toward a breeding male conspecific confined in a glass flask during the breeding season. Risk taking or boldness is indicated by positive loadings in a principal components analysis for behaviors such as early emergence from shelter, approaching the predator, and feeding in its presence. Aggression is indicated by positive loadings in a principal components analysis for behaviors such as facing the intruder and lunging at or biting it; $R^2 = 0.30$ (Huntingford 1976).

tend to avoid the predator are relatively unaggressive (Hunt-ingford 1976). A similar association between aggressiveness and risk taking has been described on a shorter timescale in juvenile sticklebacks, from at least some sites (Bell 2005), and in several other species of fish (for a review, see Huntingford and Coyle 2007). For example, risk-taking fish that inspect and bite a novel object tend to win pairwise fights against risk-avoiding fish in both juvenile brown trout (*Salmo trutta*; Sundström et al. 2004) and zebra fish (*Danio rerio*; Dahlbom et al. 2011). Where such an association exists between aggression and general risk taking, amplified predation risk can be seen as a collateral cost of an aggressive lifestyle.

The term "behavioral syndrome" has been coined to describe suits of individually consistent behavioral traits (Sih et al. 2004), the existence of which raises many intriguing questions about causes, development, and evolutionary consequences of an apparent lack of flexibility. Sometimes the term "personality" is used to describe consistent differences in suites of correlated behavioral traits in nonhuman animals (Carere and Maestri-pieri 2012). This has the very real advantage of making it easy to communicate the sort of phenomenon under discussion. On the other hand, applying a term developed to describe differences among humans to nonhuman animals, however carefully defined, potentially involves a risk of anthropomorphism and of underestimating the differences in complexity between human personalities and the behavioral phenomenon given this term in animals. It is a matter of personal opinion whether the real advantages outweigh the potential disadvantages of using this term with reference to nonhuman animals.

In some cases, suites of individually consistent behavioral traits are associated with marked physiological differences, in which case the less controversial term "stress coping styles" is often used. For example, in many species of vertebrate, there is a continuum with so-called proactive and reactive animals at the opposite extremes. Proactive animals are risk takers that show active flight-fight responses to challenge, tend to form and follow routines, and have a predominantly adrenaline-based physiological stress response. In contrast, reactive animals are risk averse, show a passive, hide/freeze response to challenge, are sensitive and respond flexibly to environmental change, and show a predominantly cortisol-based physiological stress response (Korte et al. 2005).

Some Provisos and Complications

In spite of many well-documented examples of consistent behavioral differences among individual fishes, there are also cases in which levels of aggression and/or of general risk taking are not consistent but change according to circumstances. For example, a small difference in water temperature alters relative levels of aggressiveness in damselfish (*Pomacentrus bankanensis*; Biro et al. 2010). In addition, a number of cases have been reported in which aggression and risk taking are not linked to a behavioral syndrome, for example, in populations of three-spined stickleback from sites with no piscivorous vertebrates (Bell 2005; Dingemanse et al. 2007). Interestingly, Bell and Sih

(2007) have shown that an aggression-risk-taking syndrome appears in sticklebacks from predator-free sites following a brief burst of predation, as a result of both selective predation and behavioral plasticity within a generation. As a final complication, the behavioral and physiological aspects of stress coping styles can be dissociated. Thus, the link between stress responsiveness and behavior that has been reported in rainbow trout (*Oncorhynchus mykiss*; Schjolden et al. 2005) can be dissociated, for example, following prolonged stress during transport (Ruiz-Gomez et al. 2008; Thomson et al. 2011). Risk taking differs consistently between early- and late-emerging salmon fry over the first 5 mo of life, with early emergers being quicker to start feeding in isolation. However, no differences between these two groups were found in social status, poststress cortisol levels, or resting metabolic rate, so here, too, boldness and other aspects of stress coping styles can be separated (Vaz-Serrano et al. 2011).

Functional Questions about Consistent Individual Differences in Aggressiveness

In cases where consistently aggressive, risk-taking fish do coexist with consistently nonaggressive, risk-avoiding fish, this raises a number of difficult functional or evolutionary questions. To quote Wolf et al. (2007, p. 581):

> The phenomenon of animal personality is one of the most intriguing challenges to the adaptationist paradigm in behavioral research. ... From an adaptive perspective, the evolution of animal personalities is still a mystery, because a more flexible structure of behavior should provide a selective advantage.

These difficult questions include why behavior in any one context is ever stable across time rather than being flexible, why consistent individual differences in one context are sometimes predictive of behavior in other contexts, and why animals with different behavioral styles (e.g., aggressive and nonaggressive) often coexist within a population. These questions are currently of considerable research interest (Réale et al. 2010), and there is a growing body of relevant empirical data for particular species. There are also a number of explanatory frameworks and models showing in general terms the selective forces under which these phenomena might have arisen (Dingemanse and Wolf 2010). Both help to shed light on the adaptive significance of animal personalities, using the term for brevity and convenience, and both are considered briefly here.

Empirical Examples

There is a burgeoning and complex literature documenting different kinds of effects of a given level of aggressiveness on fitness-related traits. In some cases, the effects are direct, through preferential access to food, better growth and survival, or greater reproductive success in aggressive as opposed to nonaggressive individuals. In other cases, the route from aggressiveness to fitness is indirect, acting through correlated behavioral traits such as differences in risk taking. The overall message is that a particular level of aggressiveness has many
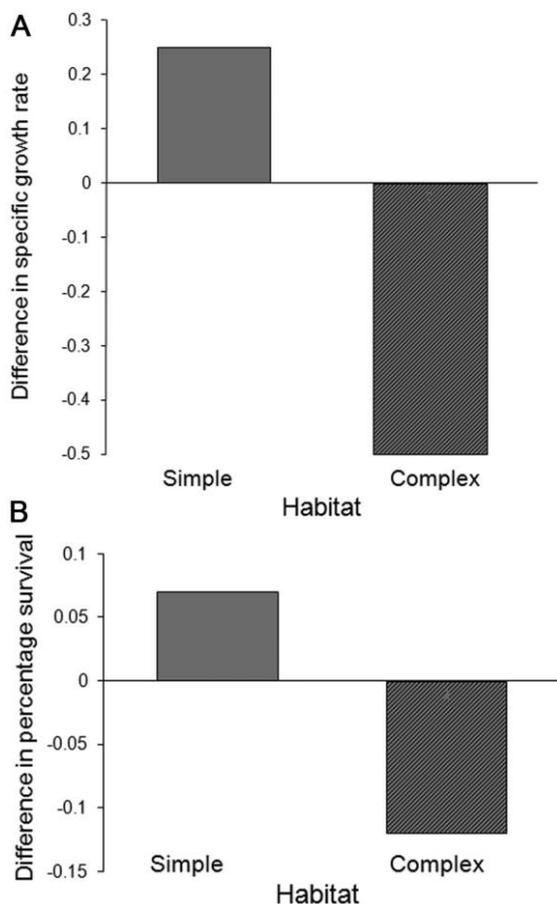
Figure 5. Mean difference between dominant and subordinate in pairs of brown trout in (*A*) specific growth rate in mass and (*B*) percentage survival, when held in groups of 10 in a stream channel with either a gravel base with three large stones (complex habitat; cross-hatched bars; $N = 15$ dominant and 15 subordinate fish) or a sand base only (simple habitat; plain bars; $N = 13$ dominant and 13 subordinate fish; Höjesjö et al. 2004).

and ramifying positive and negative effects on fitness, which vary with species, population, and gender, as well as with context. There is no generally applicable answer to why animal personalities exist and as yet no clear and complete answer for any given species. However, the fact that variable levels of aggressiveness have complex fitness consequences gives plenty of scope for different behavioral phenotypes to coexist.

Direct Effects of Level of Aggressiveness

As described above, in juvenile Atlantic salmon (Adams et al. 1998) and goldfish (Tamilselvan 2010), the most aggressive fish within a small group tend to acquire the most food. Aggressive animals often enjoy greater mating success; for example, dominant female pipefish (*Syngnathus typhle*) are particularly effective in competition for access to males with empty pouches (Berglund and Rosenqvist 2003), and among wild male Atlantic salmon, aggressiveness is associated with spawning success

(Weir et al. 2004). Numerous studies have shown that, in certain circumstances, aggressive fish grow and survive better. For example, dominant Arctic char (*Salvelinus alpinus*) have better nutrient reserves and grow faster than do subordinate fish (Le François et al. 2005). In general, aggressive fish tend to do well compared to their nonaggressive companions at high densities in simple environments with predictable food but poorly in complex environments with unpredictable food and low densities (for a review, see Damsgaard and Huntingford 2012). For example, Atlantic salmon that aggressively monopolize a spatially restricted and temporally predictable food supply and grow well when held at relatively high densities in culture tanks do much worse than their subordinate companions when moved to a more natural environment, where densities are lower and food less predictable (Huntingford and Adams 2005). In brown trout, dominant fish grow faster and survive better than subordinates in a simple habitat, but the converse is true in a more complex habitat (fig. 5; Höjesjö et al. 2004).

Indirect Effects via Correlated Behavioral Traits

Other effects of aggressiveness on fitness are indirect and associated with correlated behavioral traits, including differences in risk taking. For example, rainbow trout with a genotype characterized by fast growth, aggressiveness, and risk taking are more vulnerable to human predation in the form of intensive gillnetting than are trout with a genotype generating the opposite traits (fig. 6; Biro and Post 2008). Differences in learning and general flexibility also modulate the advantageous effects of aggressiveness. For example, rainbow trout from strains selected for high stress responsiveness (which are aggressive risk takers) and for low stress responsiveness (which are nonaggressive risk avoiders) learn equally readily to follow a visual landmark to find food in one of two potential feeding chambers. When food is then moved to a new (easily visible) position,
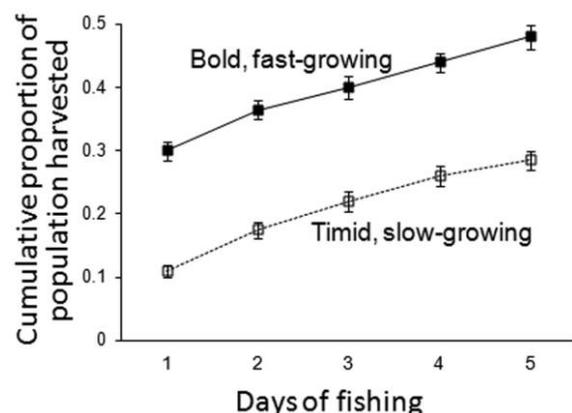

Figure 6. Mean ($\pm$ SE) cumulative proportion of rainbow trout of two different genotypes (generating fast-growing, aggressive, bold fish or slow-growing, nonaggressive, timid fish) stocked in two small lakes that were harvested by intensive gillnetting over five successive days (redrawn from Biro and Post 2008).

fish from the nonaggressive, risk-avoiding strain quickly find food in the new position, but the aggressive, risk-taking fish ignore it, going straight to the previously rewarded sign and taking a long time to feed. On the other hand, when a novel object is placed on the approach to the feeding chambers, risk-averse trout are distracted by this and take longer to feed, while risk takers ignored and carried on as usual (fig. 7). So depending on circumstances, the associated behavioral traits of both proactive and reactive fish can result in less efficient foraging, demonstrating another hidden, context-dependent cost of a given level of aggressiveness (Ruiz-Gomez et al. 2011).

Indirect Effects via Correlated Physiological Traits

As discussed above, variable levels of aggression are often associated with differences in stress physiology, which complicate the energetic costs of fighting. For example, a prolonged post-fight stress response in reactive fish would add to the metabolic cost of fighting. Levels of aggression may also be associated with differences in resting or routine metabolic rate, measured in more or less immobile fish with empty stomachs held in the dark at a fixed temperature, and in some cases this variability is consistent over time (Burton et al. 2012). In fights between pairs of size-matched, first-feeding Atlantic salmon (Metcalfe et al. 1995) and rainbow trout (McCarthy 2001), the individual with the higher metabolic rate is most likely to win. In juvenile masu salmon, *Oncorhynchus masou*, there is a significant positive relationship between metabolic rate and the ability of fish to monopolize large, profitable territories (Yamamoto et al. 1998). In common carp (*Cyprinus carpio*), proactive, risk-taking animals, which have a competitive advantage over their reactive, risk-avoiding companions, have significantly higher metabolic rates (Huntingford et al. 2010). Associated with this higher metabolic rate, proactive carp have a larger and more exposed gill surface, adding a collateral osmoregulatory cost to a proactive lifestyle (Jenjan 2011). Higher resting or routine metabolic rate and the osmoregulatory costs of a larger gill surface add collateral costs to an aggressive lifestyle. However, it should be noted that in some cases physiological differences may be the cause and not the consequence of the behavioral differences; for example, a correlation exists between risk taking and metabolic rate in sea bass after a period of fasting but not after a meal (Killen et al. 2011).

Broad Explanatory Frameworks

In this section, we describe two of the many broad explanatory frameworks that have been developed to explore the ecological and evolutionary processes that can potentially generate consistent, linked levels of aggressiveness and boldness and allow animals with different behavioral profiles to coexist. Our aim is to illustrate how such frameworks and models can help to identify the kinds of selective forces that could potentially generate these phenomena; it is not to provide an exhaustive review of the current understanding generated by such frameworks
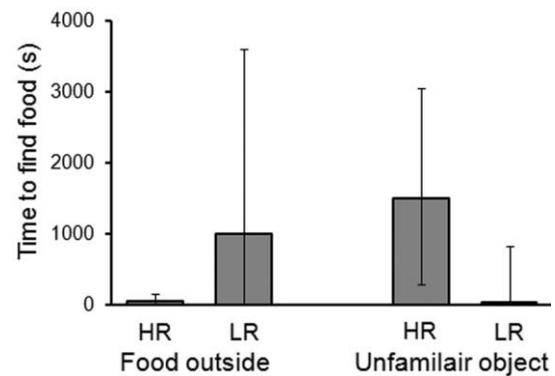

Figure 7. Median and interquartile range of the time to find food by rainbow trout from high-stress-responsive strain (HR; $N = 10$) and a low-stress-responsive strain (LR; $N = 10$) trained to emerge from shelter to find food in one of two feeding chambers when food was relocated to an open area in front of the chambers ("Food outside") and an unfamiliar object was placed on the route between the covered shelter and the maze ("Unfamiliar object"; redrawn from Ruiz-Gomez et al. 2011).

and models, which can be found in Dingemanse and Wolf (2010).

The first framework depends on a life-history trade-off between growth and mortality (Stamps 2007; Biro and Stamps 2008). It often happens that individual animals adopt a life-history pattern that involves growing fast and maturing at an early age, as opposed to growing more slowly and maturing later (Thorpe et al. 1998). The balance of fitness costs and benefits of early versus late maturation explain why the two life-history patterns coexist over evolutionary time. The different life-history trajectories may involve a number of morphological and physiological specializations, such as a large heart and respiratory structures to service the high metabolic rate needed for fast growth, as well as investment in gonadal development in early-maturing individuals. Such morphological and physiological specializations impose a cost of switching between life-history trajectories, generating consistent phenotypic differences. Aggression and risk taking come in because fast growth must be fueled by a high rate of food acquisition, which in turn involves both a willingness to take risks (e.g., foraging rather than taking shelter in potentially dangerous circumstances) and a readiness to fight over limited food supplies. Thus, the framework of a growth-mortality trade-off, seen among other instances when animals adopt different life-history patterns, can potentially explain consistent individual differences in behavior, correlated risk taking and aggression, and the coexistence of different behavioral phenotypes within populations.

The second explanatory framework to be considered here, which also involves a life-history trade-off, is the asset protection model developed by Wolf et al. (2007). This model has been criticized (Sih and Bell 2008) and developed further (Wolf and Weissing 2010); it is described here in its original form because it remains a good example of the kinds of selective

processes that could potentially account for consistent variability in aggression and risk taking and the correlation between them. According to this model, hypothetical individual animals live for 2 yr and reproduce in each year. Their habitat contains patches in which resources are gathered, which can vary from low to high quality. In year 1, all patches have low-quality resources, and in year 2, there is a mixture of low- and high-quality patches. The critical behavioral phenotype that the model investigates is intensity of exploration, which ranges from superficial to thorough. In the model there is a trade-off between future and current reproduction, mediated by the fact that a high level of exploration of potential resource patches in year 1, when patches are poor, reduces reproduction in that year but increases it in year 2, through better knowledge of the distribution of resources. Thorough exploration therefore represents investment in future as opposed to current reproduction. The model calculates the payoffs to individuals with different exploration levels in any one generation, the fitness of such individuals over successive hypothetical generations, and hence distribution of exploration levels over evolutionary time. Output from the model tells us that a trade-off between current and future reproduction mediated via level of exploration can generate populations with a stable polymorphism for this trait.

Aggression and boldness come into the model because in years 1 and 2, individuals face foraging decisions taken under predation risk, to which they can respond with either bold or shy behavior, and aggressive encounters with a conspecific, in which they can either fight fiercely (acting as hawks) or respond peacefully (acting as doves). In the risky foraging context, only bold responders get food (and so enjoy increased fecundity), but this comes at the cost of an increased probability of being eaten. During aggressive encounters, hawks get a higher payoff than doves but may be killed as a consequence of engaging in dangerous fights. Running these scenarios through the model with animals experiencing two risky foraging challenges and two fights shows that, in individuals with higher future expectations (thorough explorers), reproductive output is maximized by being consistently risk averse when foraging and consistently peaceful when confronting a rival. In contrast, individuals with low future reproductive expectations (superficial foragers) gain maximum fitness by consistently showing the converse set of traits. There is nothing in the rules of the game that forces individuals to respond consistently in successive games or to pair boldness with aggression. Instead, these traits emerge from the fitness sums generated by a trade-off between current and future reproductive success mediated by differences in exploration. This model shows how, in principle, consistent individual-specific levels of aggressiveness and boldness, as well as a correlation between them, could possibly evolve and how bold-aggressive and shy-nonaggressive individuals coexist within populations over evolutionary time.

Conclusions

There are a number of different answers to the question of why some fish fight more than others, even concentrating on func-

tional explanations relating to effects on Darwinian fitness. In many cases, some fish fight more than others because, for various reasons, compared to other fish in the same population they temporarily stand to gain greater benefits from winning (in terms of access to resources) or to experience lower costs for participating in a fight (in terms of time and energy and the risk of injury and predation). Thus, temporary and reversible differences in aggressiveness reflect responses to short-term differences in the costs and benefits of fighting. Where longer-term individual differences are concerned, questions arise as to why aggressiveness is often (but not always) consistent over time, why it is often (but not always) associated with general differences in risk taking and stress coping style, and why aggressive, risk-taking individuals often coexist with nonaggressive, risk-avoiding fish. Here, too, functional explanations involve differences in the benefits and costs of aggression, but acting over a longer timescale. The complex consequences of a given level of aggression for fitness (positive or negative, direct or indirect, context specific, and possibly frequency dependent) offer ample scope for individuals with different behavioral phenotypes to gain equal fitness and so to coexist over evolutionary time. There are a number of possible explanations for consistency in aggressiveness and for covariance between aggressiveness and boldness; life-history trade-offs, for example, between growth and mortality or between investment in current or future reproduction, are likely to be involved.

Acknowledgments

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