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Using knowledge from human research to improve understanding of contest theory and contest dynamics

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Our understanding of animal contests and the factors that affect contest dynamics and decisions stems from a long and prosperous collaboration between empiricists and theoreticians. Over the last two decades, however, theoretical predictions regarding the factors that affect individual decisions before, during and after a contest are becoming increasingly difficult to test empirically. Extremely large sample sizes are necessary to experimentally test the nuanced theoretical assumptions surrounding how information is used by animals during a contest, how context changes the information used, and how individuals change behaviour as a result of both the information available and the context in which the information is acquired. In this review, we discuss how the investigation of contests in humans through the collaboration of biologists and psychologists may advance contest theory and dynamics in general. We argue that a long and productive history exploring human behaviour and psychology combined with technological advancements provide a unique opportunity to manipulate human perception during contests and collect unbiased data, allowing more targeted examinations of particular aspects of contest theory (e.g. winner/loser effects, information use as a function of age). We hope that our perspective provides the impetus for many future collaborations between biologists and psychologists.

1. Introduction

Decades of research across a wide range of species have been dedicated to understanding the ethology of contests and the traits that predict success [1,2]. We now understand that ritualized displays in animal contests exist because escalating a fight with a competitor who may overwhelm them can cause injury or death. By assessing the displays of their opponents, contestants have an opportunity to estimate their likelihood of winning (consciously or not) and decide whether they should continue to invest energy in the current contest or acquiesce.

Little is known about the mechanisms that influence the decision of whether to compete or not. Do competitors assess their own energy reserves, and if so, are displays a war of attrition in which the loser is the individual that runs out of energy first (self-assessment models; [3,4])? Do individuals use their opponent's displays to assess their formidability, and whether they are likely to win or lose (opponent assessment models; [5])? Or do animals make even more complex decisions during contests, by both assessing their opponent and comparing this assessment with what they know about their own current fighting ability (mutual assessment models; [6])? Understanding which assessment strategies animals use, whether they modify their assessment strategies in different contexts, and the factors individuals use to make decisions within contests are some of the most-discussed questions in the contest literature [5,7–10]. Much of this discussion revolves around the extent to which animals vary their strategies (e.g. [11]) and engage in more complex comparative decision-making [7–9]. Being able to determine exactly how individuals use information to make contest-dependent, fitness-relevant decisions would provide valuable insight into both the evolution

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of various traits and strategies, as well as the selective pressures that are necessary for competitive decision-making to evolve. Hence, the challenge faced by contest theoreticians and empiricists alike is that of uncovering a more complete and general understanding of decision-making processes and their role in shaping the progression of contests.

Furthermore, behavioural and evolutionary biologists have struggled to understand how and why contest outcomes affect individuals' subsequent behaviour. Throughout the animal kingdom, empirical studies demonstrate that all else being equal, winners are more likely to win their next contest while losers are more likely to lose [12,13]. This phenomenon is known as the 'winner effect' and 'loser effect', respectively. The mechanisms underlying winner and loser effects are still unclear, and many inconsistencies regarding the effects of prior experience on contest outcomes exist in the literature. For example, although experience effects consistently occur in many animals, the strength and duration of these effects on future contest outcomes vary between species [12,13]. Additionally, experience effects in different animal species do not appear to share a common physiological mechanism [12]. Thus, it seems unlikely that experience effects are a universally evolved physiological response. These inconsistencies are further compounded by evidence that previous contest outcomes do not affect an individual's *actual* fighting ability, only their decision of whether to escalate a contest [12,14,15]. In other words, prior experience only affects how an individual behaves during the display phase of a contest, not their ability to perform during contest escalation and interactions [12,14,15], but see Condon & Lailvaux [16] for an example where losers became physically weaker. Furthermore, a recent study exploring winner and loser effects in humans suggests that winning and losing have different effects on behaviour, depending on whether contest was easily or narrowly decided [17]. On the whole, this body of work suggests that there still is much that we do not know about the causes and consequences of prior experience effects.

Recent work suggests that information use in contests is not limited to a single bout, and that the value of information may depend on both the current state of an individual and the context of the contest [18,19]. Given these insights, a more complete understanding of contest dynamics requires moving beyond understanding the individual traits and how they signal fighting ability (i.e. resource holding potential (RHP)), and the association between RHP and success. Instead, it needs the quantification of the information individuals gain from the displays of others and how this information affects their understanding of themselves, and therefore, their behaviour. For example, age and experience are theorized to affect the strength of winner and loser effects [18]. In the same manner, it is likely that the order in which an individual encounters opponents of variable strength affects how it perceives itself relative to rivals [19]. On the whole, this highlights the need to explore information exchange over time, and to not treat contests as independent events.

Although the idea that experience effects allow individuals to reassess their relative fighting ability is theoretically sound [18] and is supported by anecdotal empirical evidence [12,15], robust empirical evidence is still lacking. The latter is because exploring how perceived and actual fighting ability change as a function of experience requires an accurate measure of how individuals perceive themselves over time. Moreover, it would be beneficial if we could manipulate animals so as to separate the relative importance of perceived and actual ability on contest outcomes. Researchers could then examine how each individual interaction cumulatively affects an individual's perception of their own ability relative to rivals (and whether this perception converges towards an individual's actual fighting ability). Such data, however, are difficult if not impossible to gather in most animal systems, not only because of the sheer volume of data required, but also because it is difficult to know how individuals make decisions. These considerations are of particular relevance to a recently introduced concept in contest theory, skill. Skill is the notion that individuals vary in their ability to accurately and efficiently perform particular displays or attacks during a contest [20]. This differs from RHP and ability in that these two aspects are associated with particular traits rather than how traits are displayed. Although we may have an understanding of what skill is in human terms, whether it plays the same role in non-human contests and how skill changes over an individual's lifetime due to experience is generally not understood.

Here, we argue that behavioural and evolutionary biologists may gain novel insight into contests by collaborating with psychologists to examine human contest behaviour and dynamics (see also [21]). To make this point, we will first discuss the similarities between competitions in non-human and human animals to demonstrate why humans are a meaningful model for advancing our understanding of contests in non-human animals. We will then discuss how humans can provide an opportunity for understanding contest dynamics not available when studying other species. Finally, we highlight different methodological approaches that could be used with humans that may provide researchers with a more nuanced understanding of contest dynamics. Importantly, we do not advocate humans as a superior model species when it comes to understanding contest dynamics. Instead, we suggest that humans can provide a powerful and complementary, but so far underappreciated, model that can further research in ways that are unavailable if we limit ourselves to non-human species.

2. Contests in humans versus other animals

(a) Similar reasons for aggression and competition

In non-human animals, the factors that contribute most to the intensity of intrasexual competition are the availability of resources and the number of individuals competing for them [22,23]. These same factors also elevate forms of intrasexual competition in humans, as demonstrated in numerous hunter–gatherer societies and some non-human primates, who engage in intergroup aggression when access to resources such as food or territories is scarce [24].

Aggression in humans is also more likely among those for whom obtaining mating-relevant resources is especially relevant. In their impactful work, Wilson and Daly found that murderers are most likely to be young, male, unmarried, unemployed and lacking economic prospects [25,26], suggesting that low-status males may use violence to decrease the likelihood of competition and elevate their own likelihood of mating success. Furthermore, societies that are relatively high in economic inequality—a proxy for reproductive variance in men—also tend to be the most violent [27]. Resource scarcity and the threat of losing mating-relevant resources can thus spark aggression in non-human and human animals alike.

The risk factor that sparks the greatest intensity of competition is direct access to mates. There are many examples in the animal kingdom that demonstrate that competitions become more intense when the sex ratio becomes more male-biased [28,29], and this effect also arises in humans [30,31]. Human societies that are polygynous also generate particularly fierce competition among males because they add to the increase in variability in male fitness [32]. Indeed, there is evidence that polygynous social structure increases male mortality, sexual dimorphism and risk-taking in men [33,34]. Further support for mating pressure as a driver of intrasexual violence in humans is evidenced by data showing that men are also most violent when they are in the dating market (around 18–30 years old; [25,35,36]). Thus, although the contexts may differ, the underlying evolutionary principles of competition that are relevant for non-human animals tend to be relevant for humans too.

The same is true for the physiological underpinnings of competition and aggression in humans and non-human animals. In many non-human species, the physiological underpinnings of aggression are tied to testosterone (vertebrates) [37] or juvenile hormone (invertebrates) [38,39]. Although the relationship is much weaker in humans than many non-human animals, testosterone is linked with human aggression and status-seeking behaviour more generally [40]. Just as testosterone and aggression drop in non-human species when the mating period ends (e.g. [41]), testosterone and aggression decrease in men after they marry [42]. Increases in testosterone both before and after competition may be partially responsible for determining behavioural reactions to competition outcomes also in humans. For instance, anticipatory and post-competition increases in testosterone have been observed in winners of tennis matches [43], laboratory aggression paradigms [44] and even chess matches [45]. These results should be interpreted with caution, however, as many studies relied on small samples and there are several failures to replicate. For instance, one study of women rugby players found that the pregame rise in testosterone was associated with team bonding, aggressiveness and being focused, but not winning [46]. Nonetheless, a recent study did find that the experimental, placebo-controlled administration of testosterone inflated men's sense of their own dominance [47].

(b) Humans also assess opponent formidability

A foundation of contest theory is that individuals assess some aspect (e.g. a trait and/or a behaviour) within a contest to determine whether they should continue the contest over a resource. Even though assessment strategies should vary depending on context ([7–9], e.g. [11]), the most common form of assessment in non-human animals is self-assessment, with relatively fewer examples of opponent and relative assessment [5,8,48]. By contrast, most studies exploring human contests focus on opponent assessment (e.g. [49]) because of the ease of presenting images and asking participants to rate them, and there is less evidence for other assessment strategies. Nonetheless, other studies in social psychology demonstrate that individuals often compare themselves to others in different contexts [50–52], suggesting that humans should be quite capable of mutual assessment within contests.

Not unlike non-human animals, which use particular traits (e.g. size, weight or colour) to determine RHP, there are studies demonstrating that in humans, size (e.g. height and weight) is effectively used to assess opponents [53]. However, many of the demonstrated assessment strategies focus on human faces [53,54]. For example, one study reported that people could accurately detect aggressiveness from a face shown for just 39 ms [55]. This emphasis on facial features in humans is not unexpected, as unlike other parts of the body, the male face is usually unobscured (other than partial obscurity in males with facial hair). This feature makes the male face a particularly good cue for judging physical strength, dominance and fighting ability [49,56].

One particular aspect of the human face that people rely on to make judgements is the ratio of the face's width to height, known as the facial width-to-height ratio (FWHR; [57]). The FWHR is thought to be influenced by testosterone exposure during development and a meta-analysis found that faces of men with relatively larger FWHRs were perceived as more aggressive and dominant than men with lower FWHRs [57]. Furthermore, the FWHR appears to be a valid cue to these traits, as men with larger FWHRs are indeed more aggressive and dominant [55,57,58], as evidenced by a positive correlation between FWHR fighting success in professional combatants (Ultimate Fighting Championship fighters) [49]. Studies with human participants may thus provide researchers the ability to investigate the associations between testosterone, trait expression and aggression.

In non-human animals, a particular trait can be exaggerated by revealing more of a colour patch, showing off weaponry, or growling and manipulating facial expressions. Similarly, the shape of the human face can interact with facial expressions to display an increased intention to escalate [59]. For example, the prototypical anger expression in humans is a furrowed brow, pursed lips, raised chin, mouth and cheekbones, as well as flared nostrils [59,60]. The recalibrational theory of anger [61] posits that anger expressions signal to conspecifics that they should recalibrate their interests to the welfare of the angry person or face possible harm. Indeed, recent research manipulating angry facial expressions on digitized human faces showed that participants rated the faces with manipulated anger faces as physically stronger [60]. People also have trouble differentiating the facial expression of determination from that of anger, which could further signal that an angry person is also determined to retain the contested resource [62]. Interestingly, humans are biased towards seeing anger in people with larger FWHRs [63]. Thus, whether guarding a mate from a poaching conspecific or defending one's territory, the message signalled by a display of anger or threat of aggression is the same: *let me win the competition or face harm*.

In addition to physical properties, species such as red deer [64], baboons [65] and owls [66] use vocalizations to size up conspecifics' formidability. Similarly, humans from diverse cultures such as the USA, Romania, the indigenous Tsimane people of Bolivia and Andean herder–horticulturists in Argentina can all accurately judge upper body strength in men by listening to short clips of their voices [67] (but see [56] for a non-replication). Upper body strength is important because it is a strong determinant of fighting ability in men and correlates with a history of aggression and self-reported wins [53].

(c) Context matters

In non-human animals, the context of the competition can play an important role in the outcome of a contest; the quality of a resource is important [68,69], and ownership of it can result in males behaving as if they were 10% larger [70]. Additionally, other social factors such as whether an individual has seen or heard (i.e. eavesdropping [71]) their current rival previously win or lose and whether there is an audience [72] will affect a focal individual's level of aggression. Last but not least, the outcome of a contest can have effects on subsequent contests [12,13]. All these results suggest that the context of a contest changes the relative importance of information, and this alters an individual's behaviour before, during and after a contest.

In humans too, context influences the decision to continue a contest or not [53,54]. For example, fights often occur in the presence of prospective mates, such as in bars and clubs (probably due to the lowering of a contest threshold by alcohol) [73]. Male–male aggression also escalates in contexts where reproductively relevant resources can be taken by force and societal institutions are weak [74]. The latter effect implies that under conditions in which a loss of reputation may result in the loss of resources, men are quicker to engage in contests and escalate them. Further studies show that a prison inmate's willingness to engage in physical aggression against another inmate is influenced by their perception of the other inmate's RHP, though not necessarily in the hypothesized direction [75]. Interestingly, imagining winning or losing a contest also has powerful impacts on behaviour. For instance, just asking participants to imagine winning (versus losing) a physical fight leads men to prefer more masculine-looking allies [76]. Similarly, after being asked to imagine losing (versus winning) a physical or verbal altercation, men became more sensitive to facial cues of dominance [77]. Finally, the exploration of the massive amounts of data that are available for some sports has revealed evidence of increased aggression when teams are more similar in ability (i.e. RHP) [78], and for winner and loser effects when only exploring tie-breaks in tennis [79] (but see [80] for an overview of discussions surrounding the existence of the 'hot-hand' concept; the idea that players are more successful after a string of successes). These results suggest that not all contests are equal and that, depending on the opponent and the context, the effect of winning or losing may vary.

3. Why humans are a good model system for testing contest theory

It is because of one of the cornerstones of human cognition—theory of mind—that research on humans has the potential to significantly advance our understanding of contest behaviour and dynamics. Theory of mind is the understanding that oneself and other human beings possess mental states such as desires, beliefs, perceptions and emotions, and that these mental states have a causal relationship with events in the physical world [81]. Animals that possess theory of mind show some understanding that mental states are the causes as well as the effects of their own and others' actions [82]. For example, theory of mind includes understanding that beliefs often originate in perceptions, that desires and beliefs produce actions, and that actions can subsequently alter beliefs and desires. Animals with theory of mind are thus able to understand that individuals can form erroneous beliefs and can extrapolate the effect the erroneous belief will have on its holder [83].

In combination with the ability to think hypothetically, theory of mind allows humans to report on the beliefs, desires and perceptions which influence their real or imagined behaviour. This could provide researchers with insight into understanding which cues are assessed in animal contests. Biologists often operationalize fighting ability using one particular characteristic, such as body size, but characteristics such as these are only correlates of RHP. This fact raises the possibility that individuals may in fact assess a cue correlated to body size, or a different cue altogether [5]. Humans' ability to report on which cues affected their behaviour can provide direct insight into the relevance of particular cues to contest outcome and structure. Our enhanced visuospatial skills and ability to make inferences about others further means that humans assess (and researchers can test) a multitude of potential cues to RHP. This results in a rich foundation for understanding signal assessment and contest outcomes. Thus, even though humans' self-reports are not always accurate [84], this limitation can be overcome with specific methods (we outline these in the next section).

Another reason that humans are a good model system for understanding contest theory is the fact that humans frequently define themselves, at least in part, by comparing themselves to others [85]. Social psychological research has revealed that humans engage in self-comparison when they are uncertain of their abilities and when objective means of self-evaluation are not available [51,86]. Humans often compare themselves to individuals who are more like them [87], even if these individuals are strangers [88]. The conditions necessary for self-comparison to arise are inherent in many contests, meaning that another's performance relative to our own can alter how humans perceive their own abilities. Thus, even if an individual's fighting ability remains constant after a contest, their perception of their ability may diminish after repeated losses or increase after repeated wins (e.g. [12,13]). In combination with theory of mind, this facet of human psychology allows researchers to investigate and test hypotheses regarding perceived versus actual fighting ability, and to separate out the importance of each in guiding contest structure and outcomes.

Manipulating perceptions of fighting ability—for example, by affecting an animal's ability to signal—can also be ethically problematic (e.g. [89]). Because humans can suspend disbelief and think hypothetically, using humans in contest theory research can circumvent the ethical and methodological issues of measuring contest decision-making in non-human animals. Likewise, researchers can expose humans to repeated, continuous manipulations of cues in a short period of time (e.g. facial morphing), thus enhancing statistical power to detect effects. Comparative procedures to manipulate self-perception of fighting ability with non-human animals would be very difficult to execute.

4. Methods specific to humans

A core strength of using humans to inform contest theory is that humans can report their mental processes to others and explain how those processes guide behaviour. Although humans are generally good at attributing their behaviour to specific causes, there is evidence to suggest that when causes are subtle or not consciously available, self-knowledge can be incorrect [84]. In other words, humans are sometimes unable or unwilling to accurately report their thought processes to others, and social desirability and self-presentational biases can lead to a distortion of the truth [90–92]. Psychologists, however, have provided one solution to this problem by using implicit measures to assess psychological attributes. Implicit measures rely on psychological measurement instruments that greatly curtail participants' ability to control their responses and do not require introspective self-awareness [93]. They can test attitudes, preferences and behaviours relevant to the strategies and cues animals use to assess conspecifics.

(a) Implicit associations

One of the most frequently used implicit psychological paradigms is the implicit association test (IAT; [94]). The IAT compares associations between categories of stimuli using reaction times. Target words or images are presented on screen, and participants group the target stimuli into their respective categories at high speed by pressing computer keys. Multiple trials are conducted, and shorter average response latencies indicate stronger cognitive associations between concepts [95]. Implicit measures have been specifically designed and shown to avoid self-presentation effects and biases [90], and studies demonstrate that the IAT cannot be voluntarily controlled [91,92].

Electronic supplementary material, figure S1 shows an example of four trials from a fictitious IAT that a researcher could employ to understand the cues humans use to assess RHP. In this single-category IAT, participants are presented with a computerized male body that is morphed to accentuate asymmetries in fighting ability. Trials 1 and 3 depict men with a broad chest and shoulders and slim waist, whereas Trials 2 and 4 depict men with both narrow shoulders and hips. Likewise, Trials 1 and 2 present men that are taller than the participant, whereas Trials 3 and 4 present men who are shorter than the participant (the orange arrow indicates the participant's size, relative to the computerized male). By allocating the target male into the safe or threatening category at high speed over multiple trials, an IAT such as this provides an indication of the degree to which a participant finds particular cues to be psychologically threatening.

(b) Priming

A second paradigm is semantic priming [96]. In one example of semantic priming, the lexical decision task involves presenting participants with a meaningful prime (e.g. rich man), which is surrounded by non-word masks, followed by a test letter string which can either be a meaningful word (e.g. strong, figure S2) or a non-word (e.g. gtare instead of strong). Participants indicate whether the second letter string is a real word or a non-word as quickly and accurately as possible and responses are recorded in milliseconds. As in the IAT, multiple trials are conducted at high speed and average response latencies are recorded. If the priming word results in participants recognizing the test word strong more quickly, the prime is assumed to evoke the semantic meaning of the test letter string word. In electronic supplementary material, figure S2, this would mean that participants would associate a rich man as also being strong. Thus, semantic priming can be used to measure the psychological processes evoked by hypothesized cues to RHP. This procedure is particularly useful when the cues are not clearly physical in nature (such as wealth or behaviours). Cataloguing the processes evoked by RHP cues could provide insight into the psychological conditions under which contests escalate or are settled conventionally, by revealing the association between particular cues and psychological states that influence specific motivational tendencies.

(c) Eye-tracking technology and psychophysiology

A third and promising avenue for implicit measures to inform contest theory is eye-tracking technology. Eye-trackers provide physiological data on a subject's gaze position in real time by tracking the position of their pupils. Although eye-trackers have successfully been used with non-human animals (e.g. primates [97], peacocks [98]), it is much easier to do so in humans, as eye-trackers can be worn as glasses, situated at the bottom of a computer monitor, or built into the monitor itself. Because the object of someone's gaze corresponds with the foci of their attention, eye tracking provides an opportunity to capture how frequently subjects attend to certain stimuli and for how long, as well as how aroused they are [99].

Electronic supplementary material, figure S3 shows an example of a 'heat map' from a fictitious eye-tracking task in which participants are presented with two males in parallel. The 'hot' zones designate where the users focused their gaze with a higher frequency. By using eye-tracking technology to track participants' gaze, researchers can gain insight into the physical cues participants assess in contest situations. Such a paradigm could also include cues associated with physiology (e.g. energy reserves) or status (e.g. wealth or job title), or even details on the contestant's and opponent's previous contest victories and defeats (e.g. contest leader boards) simply by changing the information that is shown alongside the individual in an image (e.g. providing leader board statistics or salary). Eye-tracking technology could thus measure the extent to which contest decision-making is based on physiological and non-physiological cues of RHP, as well as prior experience. For example, if researchers knew exactly which traits individuals were examining, they could compare the relative differences in trait size between the participant and the hypothetical opponent that were examined for longer or shorter periods of time. This would help researchers understand which assessment strategy participants were using, whether the assessment strategy varied depending on the trait (and/or the relative difference in trait values) and whether the participant had relatively higher or lower RHP. In addition, researchers could explore whether assessment strategies differ or change with greater experience and previous contest outcomes.

Other physiological measures can provide further insight into our understanding of contest behaviour. For example, researchers could measure heart rate, skin conductance and electromyography (e.g. the startle reflex) to gain insight into sympathetic nervous system activation, physiological arousal and negative affect. For example, two contestants could be pitted together in a contest and their perception of their RHP relative to their opponent could be manipulated using various cues (e.g. through video games (see below), or by altering the size of traits of interest). Measuring skin conductance when contestants are presented with a particular RHP cue could provide insight into the subject's emotional and sympathetic responses to that specific cue. Such measures would be difficult if not impossible to use in non-human subjects and could provide important insight into the effects of potential RHP cues on psychological states and resultant motivations.

(d) Video games are a unique research platform to manipulate contests

Game-theoretic models are one of the main means through which behavioural ecologists and mathematicians have progressed contest theory [2]. In these models, players behave according to a prescribed set of rules that describe player actions. By manipulating the rules in different contexts, researchers can explore particular aspects of different models which can suggest avenues for further empirical testing. However, although it is necessary to limit the rules for computational reasons, we are now at the point where technology is so ubiquitous that we can use humans as individual players within these theoretical models without being confined to specific rules. In other words, the game-theoretic models that are used to create predictions can be used to create actual games, and we can have humans play them to test those predictions.

Video games are a particularly useful means of exploring human contests as the interactive and immersive nature of video games elicit neural [100,101], physiological [102,103] and behavioural [104,105] responses that mirror those of real contests. Evidence suggests that repeated play improves many cognitive abilities [106,107]. Similarly, individuals who play more competitive, violent games have enhanced feelings of status and mate value [108]. Humans thus seem to be using digital contests in a similar way to how non-human animals use physical contests: to gauge their own ability/attractiveness relative to the population and to determine how they should behave [109].

We see games as having the potential to provide insight into competition dynamics and the traits important in contest outcomes in two different ways. First, like sporting competitions, video games allow players to compete against one another for a specific outcome (money, experience, rewards, fame; aspects that are associated with fitness in humans). We can monitor individual performance over time, see how individual players perform against opponents of varying ability/skill and see how those contest outcomes affect future behaviours (such as the likelihood and time taken to engage in a subsequent contest or how likely individuals are to win or lose in a subsequent contest). If an individual's ability or performance is easily assessable by opponents, perhaps through the presence of a numerical indicator (e.g. level) or through character design (e.g. traits), researchers could easily manipulate how an individual views an opponent (as potentially stronger/weaker) and/or how others view that individual. In this sense, researchers could manipulate an individual's perception of their RHP without altering their actual RHP. Given that individuals can never perfectly know their actual fighting ability, manipulating perceived and actual RHP will provide insight into how individuals learn about their own fighting ability. This will further help to explore how different experiences shape how an individual's self-perception of their ability changes as they gain experience and whether shifts in actual and perceived RHP change how individuals behave and assess opponents. Video games can also be programmed to provide a specific outcome regardless of performance (e.g. [110]), further allowing the examination of the effects of skill/performance and contest outcome on self-perception of ability. Likewise, using video games may result in a straightforward way to track how perceived ability changes relative to actual ability as individuals gain greater information from repeated competitive encounters.

Video games also provide the opportunity to explore the concept of skill and its importance to contest outcome more clearly. For example, in non-human animal contests, it is difficult to separate skill from experience as greater experience in contests is likely to improve an individual's ability to perform a behaviour simply through practice/exercise [111]. But in video games, it is simple to provide individuals with different training scenarios crossed with a string of different contest experiences. This would help researchers explore the relative role that skill, practice and contest experience have on future contest outcomes, an individual's self-perception and an individual's likelihood to re-enter a contest.

A second way to explore how individuals value certain traits or behaviours and how those traits are viewed by individuals of different skill/ability is to provide individuals with an opportunity to create their 'optimal' character in different contexts. For example, if players are given a character and a specific number of points to allocate towards different traits (e.g. size, weight, weaponry, behaviours), we can see how that allocation varies as a consequence of the social context (e.g. sex ratio, variation in resource quality, rewards to contest outcomes) or their perception of themselves (e.g. their digital or real-life performance). Coupling this approach with eye-tracking software and other psychological techniques such as priming would allow researchers to explore how individuals use traits as indicators, the threshold a trait must pass to be considered different and how context affects these aspects.

An added bonus to using video games is that there are millions of gamers throughout the world, thus providing an enormous sample size to explore contest dynamics. Given that there are also numerous video games already on the market, researchers have the opportunity to use existing game data to explore contest theory in analogous ways to using sports. As video games become cheaper to create and more immersive, it may be feasible for researchers to create games to explore specific questions in contest theory.

5. Conclusion

Over the last few decades, the exploration of animal contests and what makes a winner or a loser has seen a shift from understanding how contests progress, to how animals use information within contests to make decisions. Here, we have argued that there are limitations to what we can learn by focusing solely on non-human animals, and that through the adoption of a host of technological advances more generally and methodological advances developed by psychologists, humans can provide behavioural and evolutionary biologists with a unique perspective on how animals use information, how this information affects self-perceptions over time and how these self-perceptions alter behaviour.

Both human and non-human research into contests demonstrates that individuals do not have perfect information about themselves or their opponents, and that new information alters their future behaviour. Thus, winner and loser effects may be a behavioural shift caused by the individual learning more about themselves relative to the population of individuals they are interacting with. Experience effects as a behavioural response may explain why universal physiological underpinnings have been difficult to discover, and why winning and losing streaks last different lengths of time and vary in their strength in different species. It may be that winning and losing provide different information to participants depending on the context, their RHP and the individual's expectation entering that contest (e.g. [17]). By increasing interactions between biologists and psychologists, and by using each other's sophisticated toolbox, biologists and psychologists will be able to make great strides towards an improved general understanding of contest theory and dynamics.

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