Review

Assessment during Intergroup Contests

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Research on how competitors assess (i.e., gather information on) fighting ability and contested resources, as well as how assessment impacts on contest processes and outcomes, has been fundamental to the field of dyadic (one-on-one) contests. Despite recent growth in studies of contests between social-living groups, there is limited understanding of assessment during these intergroup contests. We adapt current knowledge of dyadic contest assessment to the intergroup case, describing what traits of groups, group members, and resources are assessed, and how assessment is manifested in contest processes (e.g., behaviors) and outcomes. This synthesis helps to explain the role of individual heterogeneity in assessment and how groups are shaped by the selective pressure of contests.

The Central Role of Assessment in Animal Contests

Animal contests determine access to crucial resources such as territory, food, and mates. Because contest outcomes result in the unequal distribution of resources (e.g., mating opportunities [1]), contests influence resource ecology. In addition, traits such as dynamic displays [2] and exaggerated weapons [3] are thought to evolve, in part, under the selective pressure of contests. Much of our knowledge of contests has come from studies of **assessment** (see Glossary), or information-gathering, during **dyadic contests** between individuals. Models of dyadic contests, which have usually been validated using evolutionary game theory [4], and experimental tests of these models (reviewed in [5]), show how individuals assess intrinsic traits (behavioral, morphological, physiological) of themselves and/or their competitors, as well as extrinsic factors (e.g., resources). In turn, this assessment influences strategic decision-making such as the decision to give up a contest (Box 1). We term this suite of models and corresponding approaches for experimental tests the **dyadic contest assessment framework**.

More recently, there has been rapid growth in the field of **intergroup contests** – contests between groups of social-living organisms. This work has been driven, in part, by attempts to understand human conflict [6,7]. Intergroup contests are also widespread in non-human organisms, including bacteria (multiple species) [8], ants (e.g., harvester ants *Messor barbarus*) [9], eusocial shrimps (*Synalpheus* spp.) [10], birds (e.g., acorn woodpeckers *Melanerpes formicivorus*) [11], and non-human primates (multiple species) [12]. Research into intergroup contests has generally focused on group member participation in conflict, and some work has also studied variation in conflict intensity [13–16]. Our understanding of assessment during intergroup contests – how groups gather information on themselves, each other, and/or contested resources, and how that information is used to make group-level decisions – is still underdeveloped [17].

Adapting the Dyadic Contest Framework to Intergroup Contests

The power of a rich history of dyadic contest research is the availability of a well-established framework that can be readily adapted to intergroup contests. The dyadic contest assessment framework can be studied through theoretical and empirical exploration of its individual components (Figure 1, Key Figure). These components include how competitors assess fighting ability and the ownership and value of contested resources, and how assessment is modified by prior

Highlights

The dyadic assessment framework – studying the strategies animals use to gather information during one-on-one contests, and how this assessment drives contest behaviors and outcomes – can be fruitfully adapted to intergroup contests: those between stable social-living groups.

Heterogeneity among group members and how groups cohere to make effective decisions are unique features of social living that add complexity to intergroup contest assessment.

Understanding intergroup contest assessment can inform research in social evolution and ecology, for example, by revealing selective pressures on group size evolution and drivers of population dynamics.

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Box 1. Dyadic and Intergroup Contest Assessment Theory

Both dyadic and intergroup contests are associated with specific theories that make predictions regarding how contests should proceed. However, the focus of those predictions differs between the two types of contest. Dyadic contest theory usually generates predictions about within-contest changes in the intensity of fighting, based on assumptions regarding the adaptive value (that is in some but not all cases verified as an evolutionarily stable solution) of various assessment strategies. By contrast, intergroup theory makes predictions about **attrition rates** experienced by the weaker side, based on assumptions about the effect of using a numerical advantage in two distinct ways (see below).

Dyadic contest theory has a long history at the core of behavioral ecology [38]. Empirical work has focused on directly testing the assumptions, and sometimes the predictions, of three models: the sequential assessment model (SAM) [66], the energetic war of attrition (EWOA) model [50], and the cumulative assessment model (CAM) [82]. The SAM assumes that each rival compares its own resource holding potential (RHP) with that of the opponent, and losers give up when they know they are weaker ('mutual assessment'). The EWOA and CAM assume that losers give up when the accumulated costs cross a threshold ('self-assessment'). A correlational approach described by Taylor and Elwood [78], as well as analyses of contest behavioral progressions [83], are often used to distinguish between these two assessment rules (Figure I), although many contests may fall outside this dichotomy [72,77].

Intergroup contests are considered by a body of theory spanning third-party interventions up to conflicts between larger groups (reviewed in [13,17]). In the latter case, key ideas come from Lanchester's attrition laws developed during World War I. These models consider how superior numbers could be best utilized when armies have access to ranged weapons. If extra numbers on the more numerous side are held in reserve until needed (i.e., the more numerous side matches the number of combatants and/or materiel allocated by the less numerous side), then Lanchester's linear law should be followed (Figure I). Lanchester's square law would be followed if the more numerous side commit their extra numbers to the fray, such that members of that side can concentrate their attacks on the outnumbered members of the weaker side (Figure I).
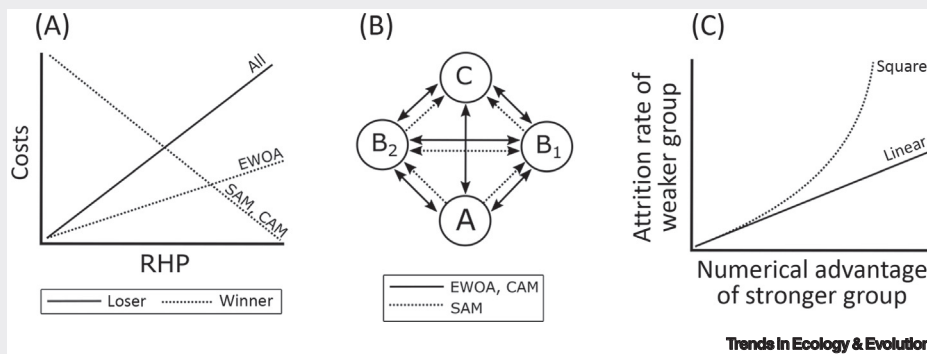

Figure I. Analyses to Differentiate between (A,B) Dyadic Contest Models and (C) Lanchester Models of Intergroup Contests. (A) The assumptions of all dyadic models predict a positive correlation between costs and the resource holding potential (RHP) of the loser (solid line). For correlations between costs and winner RHP (broken line), sequential assessment model (SAM) and cumulative assessment model (CAM) predict a negative correlation, whereas the energetic war of attrition (EWOA) indicates a weak, positive correlation. (B) EWOA and CAM (solid lines) predict that competitors can use any behavior at any point during the contest, whereas SAM (broken lines) predicts that behaviors progress in escalating phases without de-escalation. Circles represent behaviors, arrows indicate transitions between behaviors. (C) Lanchester's linear law (solid line) predicts that the attrition rate of the weaker group increases linearly with an increase in the stronger group's numerical advantage, whereas the square law (broken line) predicts that attrition rates increase with the square of stronger group numerical advantage.

experience. The framework shows how these components integrate to affect contest costs, behaviors, and outcomes, with impacts on ecology and trait evolution (Figure 1).
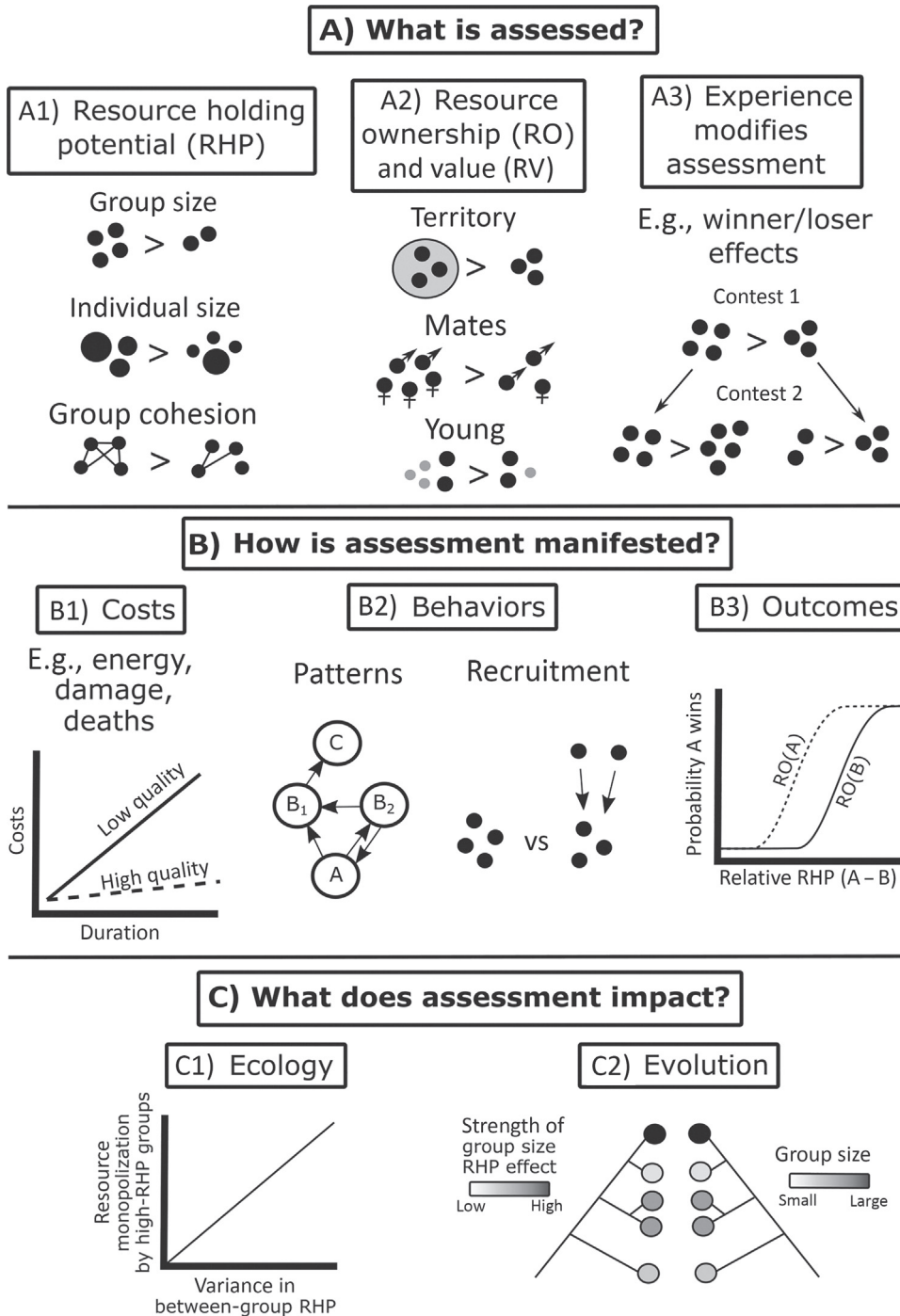
What Is Assessed?

Resource Holding Potential

Before a boxing match, commentators describe the 'tale of the tape' for both competitors, outlining size-based metrics such as weight, height, and reach that are thought to be associated with fighting success. In dyadic contest research, similar metrics describe what Parker [18]

Glossary

Assessment: information-gathering and processing. In the context of contests, assessment usually regards ability or resources and can be influenced by experience.

Attrition rate: rate of death of individuals in a group. This is used to differentiate among Lanchester's law models of intergroup conflict (Box 1).

Collective action problem: an occurrence wherein not all group members may participate in a collective effort, but success depends on collective behavior. For example, not all members of a larger group will join in an intergroup conflict, thereby reducing the group size advantage.

Dyadic contest: a direct interaction between a pair of individuals where each attempts to exclude the other from access to an indivisible resource unit.

Dyadic contest assessment framework: a set of theoretical models, with corresponding experimental approaches for testing model predictions and assumptions, that describe how competitors assess ability and resources to resolve dyadic contests.

Heterogeneity: variation among group members, for example, in sex, resource holding potential, resource ownership, resource value, or experience.

Intergroup contest: a direct interaction between two groups of social-living animals, each composed of two or more individuals, where each group attempts to exclude the other from access to an indivisible resource unit. An intergroup contest can consist of multiple dyadic contests between individuals of opposing groups.

Lanchester's laws: theoretical models of intergroup conflict defined by attrition rates.

Resource holding potential (RHP): the absolute fighting ability of an individual or group.

Resource ownership: which individual or group owns a contested resource or resources (e.g., a territory, a mate, food resources) at the beginning of a contest. Also termed 'prior residency'.

Resource value: the value of the resource to each opposing individual or group. Ideally measured in fitness units, for example, the increase in reproductive success that an individual or group would achieve from gaining or defending a contested resource.

Key Figure

A Framework for Assessment during Intergroup Contests

Social cohesion: how much or well a group acts as a unified force. Can be measured by temporal and/or spatial coordination of group member behaviors (e.g., via social networks) or other metrics.

A) What is assessed?

A1) Resource holding potential (RHP)

Group size

Individual size

Group cohesion

A2) Resource ownership (RO) and value (RV)

Territory

Mates

Young

A3) Experience modifies assessment

E.g., winner/loser effects

Contest 1

Contest 2

B) How is assessment manifested?

B1) Costs

E.g., energy, damage, deaths

Low quality

High quality

Costs / Duration

B2) Behaviors

Patterns

C
B₁ ↔ B₂
A

Recruitment

vs

B3) Outcomes

Probability A wins

RO(A) RO(B)

Relative RHP (A – B)

C) What does assessment impact?

C1) Ecology

Resource monopolization by high-RHP groups

Variance in between-group RHP

C2) Evolution

Strength of group size RHP effect

Low   High

Group size

Small   Large

Trends in Ecology & Evolution

(See figure legend at the bottom of the next page.)

termed **resource holding potential (RHP)**, defined as 'absolute fighting ability'. RHP is a theoretical concept that is often measured by proxy as the single variable that best predicts contest success [19] (Table 1). Most commonly this is body mass [19]; other proxies include weapon size [20] and physiological capacity [21]. The behaviors important to a given contest system have been thought to drive RHP proxies; for example, systems where contests involve frequent physical contact might find force output the best RHP proxy, whereas systems where competitors avoid contact might find endurance-based RHP proxies, such as fat or glycogen reserves, more important [22]. A recent meta-analysis, however, found no support for this functional approach in arthropods [23]. Though often measured as a single trait, RHP may instead be a composite of many morphological, physiological, and/or behavioral traits. For example, boxing success is not determined by reach alone, but likely by a combination of weight, height, reach, skill in delivering punches, and other factors.

The best-supported single RHP proxy in intergroup contests is group size: the number of members in each group. A recent meta-analysis affirmed this in primates [12], and group size is relevant in other taxa from ants (e.g., wood ants *Formica rufa*) [24], to lions (*Panthera leo*) [25], to birds (green woodhoopoes *Phoeniculus purpureus*) ([26]; *cf* [27] where group size does not predict outcomes in greater anis *Crotophaga major*). However, proxies other than absolute numbers might be important. A functional approach might predict that total group mass is a better RHP proxy than group size in contests that involve high levels of physical contact. Other metrics of intergroup contest RHP reveal the importance of within-group **heterogeneity** (Box 2). For example, although group size was an RHP proxy in grey wolf (*Canis lupus*) intergroup contests, groups with more males could overcome a group size disadvantage [28]. Males are larger and more aggressive than females, suggesting a functional reason for the impact of group heterogeneity on RHP. Finally, group **social cohesion** could also be a proxy of intergroup contest RHP – groups that execute contest behaviors in a more coordinated fashion may be more likely to win. Exactly as for dyadic contests, RHP for intergroup contests is likely a suite of traits comprising – within and among group members – morphology, physiology, and behavior.

Previous fighting experience can impact on how animals assess their own RHP and/or that of their opponent (Table 1). One well-known example in dyadic contests, with building evidence in intergroup contests, is winner and loser effects (Figure 1), in which winners of contests are more likely to win future contests, and losers to lose (reviewed for dyadic contests in [29]). Winner and loser effects are often observed in the behaviors used in subsequent contests. For example, male redbellied woodpeckers (*Melanerpes carolinus*) that won simulated (via playback experiments) contests gave more territorial displays to future simulated intruders [30]. In intergroup contests, winner

Figure 1. For a Figure360 author presentation of Figure 1, see the figure legend at https://doi.org/10.1016/j.tree.2020.09.007. Competing groups may assess (A1) resource holding potential (RHP), (A2) resource ownership (RO), and resource value (RV). (A3) Experience modifies the assessment of RHP, RO, and RV. In (A1–A3), filled circles represent group members; the left-hand group in each scenario is predicted to win (indicated by >). In (A1), RHP proxies include group size (number of circles), individual size (size of circles), and group social cohesion (number of lines connecting circles, as in a social network). In (A2), resource ownership (territory) or resource value (mates, young) can determine group success. (A3) A winner and/or loser effect; the winner of contest 1 wins contest 2, and the loser of contest 1 loses contest 2. (B) Assessment is manifested in (B1) the costs (e.g., energy, damage, death) paid by groups and group members (the plot shows the prediction that costs increase with contest duration differently for individuals of high and low quality); (B2) behaviors, including patterns of contest behaviors (open circles represent behaviors, arrows indicate transitions between behaviors) or individual recruitment (filled circles represent individuals, arrows indicate recruitment of individuals to smaller group); and (B3) contest outcomes (the plot indicates that relative RHP predicts the probability of contest success, e.g., of group A over group B, in a manner that is modified by RO). (C) Assessment impacts on (C1) ecology and (C2) evolution. (C1) Prediction that resources become more heavily monopolized by high-RHP groups as variance in between-group RHP increases. (C2) Prediction that, across taxa, group size evolution may correlate with the strength of the effect of group size on contest success.

Table 1. The Definition and Importance of Key Concepts in Animal Contests, Examples from Dyadic Contests, and Equivalent Examples and Peculiar Features of Intergroup Contests

Concept	Definition and importance	Dyadic examples	Intergroup equivalents	Intergroup peculiarities
Assessment strategy	Strategy of information-gathering about ability and/or resources; influences decision-making (e.g., retreat vs stay in contest)	Sequential assessment; (energetic) war of attrition; cumulative assessment (Box 1)	Lanchester's linear and square models (Box 1); dynamic contest models (Box 3)	May occur at the level of individual or at the level of the group (e.g., dyadic and intergroup assessment models may both apply)
Resource holding potential (RHP)	Absolute fighting ability; variation with costs is used to differentiate between assessment strategies (Box 1)	Body mass; weapon size; physiological capacity; skill or vigor	Group size (number of members); cohesion; traits of individuals (as in dyadic)	Heterogeneity among members is likely important
Resource ownership (RO)	Ownership of contested resource; influences motivation	Territory; shelter; mates; food	Territory; shelter; mates; food	Motivation may vary among group members according to sharing rules and time spent owning the resource
Resource value (RV)	Perceived value of the contested resource; influences motivation	Territory and/or shelter (size, quality); mates (size, fecundity); food (amount, quality); hosts (size, for parasitic spp.)	Territory and/or shelter (size, quality); mates (size, fecundity); food (amount, quality)	Motivation may vary among group members according to sharing rules
Contest experience	Prior experience in a contest (e.g., winner and loser effects) may influence the assessment of RHP, RO, and RV	Future fighting success; contest behaviors; physiology (e.g., hormone secretion)	Future fighting success; contest behaviors; physiology (e.g., hormone secretion); movement post-contest (e.g., toward territory center); within-group behaviors (e.g., grooming)	More study is needed of effects on future fighting success; experience and effects may differ among members; both intra- and intergroup conflict may affect experience
Costs	Variation with RHP is used to differentiate between assessment strategies (Box 1); assumed to increase with contest duration	Energy; damage (physical or physiological); risk of death (owing to contest or predation)	Energy; damage (physical or physiological); risk of death (owing to contest or predation)	May accrue differently for different group members (e.g., dominants vs subordinates); death is more common in intergroup contests
Behaviors	Execution incurs costs; patterns of behaviors are used to differentiate between assessment strategies (Box 1)	Signaling; exerting force (e.g., biting, pushing) with body and/or weaponry	Signaling; exerting force (e.g., biting, pushing) with body and/or weaponry; recruitment of group members; cohesive behaviors (e.g., grooming)	Individual behaviors may impact on group-level behaviors (e.g., signals inducing recruitment)

and loser effects have been inferred through movement patterns. For example, losing groups used the area in which the contest occurred less frequently [31], moved faster and further than winning groups [32], or slept closer to their territory center ([33]; cf [34] where losers slept closer to the territory boundary). Although these behavioral changes imply a loser effect, none of these studies tested whether losing groups actually lost, or winning groups won, future contests – a key component of establishing winner or loser effects.

In the same way as understanding dyadic RHP helps to develop hypotheses for how contests influence trait evolution (e.g., animal weapons [35]), studies of intergroup contest RHP and its assessment can reveal selective forces that act on group living. For example, a competitive advantage of increased group size may lead to the evolution of larger groups (Figure 1).

Resource Ownership and Value

Which competitor owns a contested resource [36] and the value of the resource to each competitor [37] is a central feature of dyadic conflict that also plays an important role in intergroup contests (Figure 1). These **resource ownership** (also termed 'prior residency') and **resource value** effects essentially modify fighting ability by affecting motivation (Table 1). Competitors that begin the contest as resource owners may have more information about the resource than non-owners, and therefore be more motivated to keep it [38]. Similarly, competitors that value a resource more may be more motivated to keep or win it. For example,

> ### Box 2. Unique Problems of Intergroup Contests
>
> Intergroup contests are characterized by two features, heterogeneity and social cohesion, that play no role in dyadic contests. Unlike individuals, groups are inherently heterogeneous, being composed of individuals that vary in size, strength, genetic relatedness, and the value they place on contested resources. Group resource holding potential (RHP) is thus determined by both individual attributes and social cohesion – that is, the degree to which group members act together. Heterogeneity is the source of the collective action problem (CAP), where group success depends on collective effort, but the costs of effort are borne by the individual [84]. Individuals that are weaker or place lower value on a contested resource are predicted to free-ride on the effort of their stronger or more incentivized group mates [85]. The CAP hinders the evolution of collective aggression, particularly in large groups that are not bound tightly by kinship or ecological constraints [57,86,87].
>
> The CAP, like other social dilemmas [85], can be overcome by coercion or inducements to cooperate. Among Turkana warriors, for example, desertion or cowardice during intergroup raids is later punished by severe beatings and the extraction of fines [88,89]. In some non-human animal societies, participation in collective conflict is encouraged through affiliative behavior during or after an intergroup encounter [90–92]. Punishment is particularly effective in asymmetric relationships where the benefits of collective action flow back to the punisher [93–95]. In general, hierarchical societies are less vulnerable to the CAP because high-ranked individuals, who gain the largest share of the fitness benefits of contests, are predicted to overcompensate for free-riding by low-ranked individuals [16].
>
> Strong social cohesion may leave heterogeneous groups vulnerable to the emergence of 'exploitative' leaders, who may initiate conflicts that benefit themselves but not the rest of the group [96]. Exploitative leadership is predicted when leaders gain greater benefits or suffer lower costs from conflict than other group members, but where there are strong constraints against desertion. In such circumstances, selection acting on leaders can lead to damaging levels of intergroup conflict, with negative consequences for population fitness. This model can explain violent intergroup conflict in banded mongooses, a species in which females lead groups into contact with rival groups and instigate intergroup contests in which males disproportionately bear the costs of fighting [96]. The decoupling of leaders from the costs they incite may be one of the evolutionary causes of extreme intergroup aggression.

subordinate fallow deer (*Dama dama*) may be so motivated to achieve rare mating opportunities that, during contests with dominants, they avoid low-cost visual signaling and escalate directly to high-cost antler clashes. In other words, there is evidence of a 'desperado effect' [1].

Territory may be the most common resource over which groups fight, and may therefore be the most common resource assessed during intergroup contests (e.g., [27,39,40]). Territory ownership and value effects may vary with where on the territory the contest occurs, for example, at the territory center versus its boundary [40,41]. However, as observed by Parker [18], territory *per se* is not always what competitors fight over; instead, they may fight over the food, mates, or other resources that the territory holds. As an example, groups might value a small territory with dense food resources or ample shelter more than they do a large territory with sparse food and shelter. Therefore, future research into resource effects in intergroup contests should consider both territory as well as the resources contained therein (e.g., [42]). For example, banded mongoose (*Mungos mungo*) intergroup contests occur at territory boundaries [43], and contests are more frequent when females are in estrus [44]. Behavioral observations have shown that estrus females seek out males from neighboring groups, resulting in intergroup contests during which females often mate with males from the neighboring group [43,45]. The contested resource is thus not territory alone, but instead a mix of territory, females, and extra-group mating opportunities. Among-individual heterogeneity in resource assessment is likely to be important: in banded mongooses, older males mate-guard estrus females more often than younger males [46]. Compared with younger males, these older males may be more motivated to fight off rival males from neighboring groups to protect their investment in gaining paternity; they may therefore fight harder. Following from this, the relative proportion of young to old males in a group may influence resource value and contest success.

Because losing groups lose both territory and the resources it contains, there may be an interaction between loser effects and resource value in intergroup contests. If losing groups lose

subsequent contests, as expected via a loser effect, they might eventually run out of energy or territory, reaching a threshold at which the group must disband. This effect might be exacerbated if the same winning group repeatedly encounters the same losing group. The impact of loser effects on resource loss could lead to selection on groups to avoid losing, for example, by heightening resource value, avoiding contests with much stronger neighbors, or by increasing breeding effort to increase group size (if group size is an RHP proxy), among other possibilities.

How Is Assessment Manifested?
Contest Costs
How competitors assess RHP and resources can be revealed in the types and amounts of costs losers are willing to incur before they give up the fight (Figure 1). Indeed, one way by which dyadic assessment strategies are parsed apart is through correlating cost accrual with RHP (Box 1). In the same way as for RHP, contest costs have been measured by many proxies, including the energy required to produce behaviors (reviewed in [47]), damage from opponent behaviors [48] or one's own behaviors [49], or simply the time allocated to the contest before a loser gives up that cannot be spent on other tasks [50] (Table 1). Most empirical studies use contest duration as a cost proxy, assuming that longer fights are costlier (e.g., in terms of energy) than shorter ones [51]. Some studies have found that what we might assume are costly contest behaviors may not have high energetic [21,52] or damage [53] costs. In these scenarios, another useful cost metric might be risk of predation [54].

Intergroup contest costs can come at the level of the individual and the group. Individuals may suffer time, physiological, or damage (including death) costs. Group costs might simply be the sum of these individual costs. Alternatively, costs may accrue in a nonlinear fashion, a factor only recently considered in dyadic contest theory [49,55]. Nonlinear cost relationships might be found if, for instance, costs to particular group members (e.g., dominant males or reproductive castes) have a disproportionate impact on group competitive ability. McAuliffe and colleagues [56] detail examples of human small-scale society warfare in which 'key individuals' participate more in conflicts and have a greater risk of being killed. Costs to these individuals may have a stronger effect on group success than costs to other group members. Other individuals may decide not to pay costs by not engaging in the contest in the first place. These **collective action problems** are one feature that is commonly considered in models and empirical studies of intergroup contests, especially in humans and non-human primates [16,57,58] (Box 2). Finally, for a given individual, the fitness costs of injury to or death of another group member might be influenced by their relatedness to that member.

Extreme costs of competition, including death, appear to be more common in intergroup than dyadic contests. Intergroup contests can regularly result in the death of adults and young in taxa as diverse as bacteria (multiple species) [8], ants (e.g., fire ants *Solenopsis invicta*) [59], termites (e.g., *Zootermopsis nevadensis*) [60], banded mongooses [44], grey wolves [61], and chimpanzees (*Pan troglodytes*) [62]. Indeed, variation in the rates of group member death is a key feature used to discriminate between different **Lanchester's law** models of intergroup conflict (Box 1). In dyadic contests, by comparison, lethal fighting is only predicted when the value of the contested resource is so high as to make the value of any future without the resource essentially zero [63]. This occurs, for example, when mating opportunities are so rare that it is worth fighting to the death over access to an unmated female [64]. The reasons why lethal fighting may be more common in intergroup than dyadic contests are underexplored. One explanation might be that although each individual may use sublethal fighting tactics during intergroup contests, multiple individuals using these tactics on a single opponent (i.e., 'ganging up' on a single opponent) could result in lethal costs. Another reason might be that individuals that lead or

instigate intergroup contests face lower costs than other group members, such as when generals send troops to war from the safety of a military base (Box 2). Finally, this trend could be an artifact of the current set of organisms in which intergroup conflict has been studied – given more work in this area the prevalence of extreme costs may be found to decline.

Aggressive Behaviors

How competitors alter behaviors during a contest can help to reveal assessment strategies and the costs that competitors are willing to incur (Table 1 and Figure 1). Importantly, behaviors are not costs in and of themselves; instead, particular behaviors might incur higher costs than others. For example, competing mantis shrimp (*Neogonodactylus bredini*) dyads escalate from visual signaling to the ritualized exchange of high-force strikes, rarely returning to the behaviors they used before. These behavioral patterns match the predictions of the sequential assessment model [65,66] in which competitors use ever-costlier behaviors to assess relative ability more accurately. Different behavioral patterns are predicted by other models of dyadic assessment (Box 1).

Assessment strategies during intergroup contests can similarly be shown by group and individual competitive behaviors. For example, during contests with heterospecific competitors, larger groups of the stingless bee *Trigona spinipes* more often direct aggression toward vital areas on their opponent's bodies (e.g., the head instead of the appendages), suggesting that groups assess an RHP advantage and attempt to maximize the costs they inflict to their weaker opponents [67]. Variation in signaling behaviors can also indicate an assessment strategy. Green woodhoopoe groups compete using vocal rallying, iteratively matching the intensity of each other's collective calls. Although short contests were won by territory residents (showing a resource ownership effect), contests lasting longer than 15 minutes were won by groups with more members [26]. In long contests, smaller groups might lose not by assessing relative RHP and deciding to give up, but instead because they reach a physiological limit beyond which they cannot continue to match the vocal rallies of their larger opponents [26], a strategy matching self-assessment models (Box 1).

Contest behaviors may vary within a group if members differ in the costs of competition. During intergroup contests in vervet monkeys (*Chlorocebus aethiops pygerythrus*), for example, there is a conflict of interest between the sexes: females with infants benefit from the resources gained by winning a contest, whereas male sires must avoid the costs of competitive injuries so they can continue to protect their young [68]. This conflict of interest results in reciprocal punishment: females use within-group aggression to induce male group-mates to fight [69], whereas males use within-group aggression to coerce females to avoid future fights [68]. Incentives, not only punishment, are important: females reward fighting males with affiliative behavior [69]. Overall, individual variation in intergroup contest behaviors is poorly understood in both theory and practice. For example, Lanchester's law models assume that all group members use the same tactics throughout the contest ([70]; examples of intergroup contest models that incorporate within-group heterogeneity are given in [13]). Recent developments in individual tracking software (e.g., [71]) can help experimentalists to quantify individual-level variation in behavior during intergroup contests, and this might feed back to influence theory.

Biases in the Study of Assessment Strategies

Whether studying behaviors or costs, researchers should avoid biases in what we think animals can assess during contests. For instance, it seems obviously advantageous to gather information on relative ability (mutual assessment, Box 1) than to not integrate information about opponent ability (self-assessment, Box 1). This might lead researchers to think that animals should, and

therefore do, assess relative ability. However, for many animals and animal groups, sensory or ecological constraints may limit assessment. In these cases, self-assessment or mixed assessment strategies may be more likely [72–74]. Furthermore, assessment strategies might fall somewhere along a continuum of self to opponent assessment, instead of into the simpler boxes established by theoretical models [72].

Perception may place another constraint on assessment strategies. One example is Weber's law, which suggests that animal sensory systems process information proportionally, not absolutely [75]. A resulting prediction is that competing groups should more accurately assess group size differences when groups are small than when they are large. For example, it is easier for a group of four to assess that they are larger than a group of three than it is a group of 40 to assess that they are larger than a group of 39, even though the absolute magnitude of the group size difference (one) is the same. This prediction found support in a test of intergroup contests in free-ranging dogs (*Canis lupus familiaris*) [76].

Contest Outcomes

Although the impact of RHP and resources on costs and behaviors is the most common way of understanding contest assessment, variation in outcomes is also a powerful tool for knowing what is assessed. This is not only because the ultimate endpoint of assessment is that it determines which individual or group leaves the contested area and which remains. Outcomes are also important for establishing RHP proxies [19], and because differentiating among assessment strategies often involves testing cost–RHP correlations separately for contest winners and losers [77,78] (Box 1). One example comes from a recent study in meerkats (*Suricata suricatta*). Although group size is the best predictor of contest success among meerkat groups, groups with pups can overcome a group size disadvantage to win the contest [33]. Groups with pups might have a motivational advantage related to resource value: winning new territory can result in more food for developing young [33].

A fascinating area for future research is how aggressive tactics (e.g., behaviors) themselves might determine contest outcomes. Briffa and Lane [79] describe, for dyadic contests, how choosing the most appropriate behavior not only reveals assessment strategies but might also influence contest success. For example, a hermit crab (*Pagurus bernhardus*) can choose to rap its shell against a competitor or to rock the competitor's shell back and forth. When rapping becomes ineffective, hermit crabs that switch to rocking not only show evidence of mutual assessment but may also increase their likelihood of winning [80]. One example of tactics in intergroup contests might be in the timing of recruitment. Recruiting group mates to join the fight too early might increase the likelihood that these individuals are unnecessarily injured, or might create too large of a group size advantage, resulting in a collective action problem. On the other hand, waiting too long to recruit could result in losing the contest before reinforcements arrive. Results from turtle ants (*Cephalotes rohweri*) suggest that this species recruits soldiers according to the defensibility of nests. Turtle ant colonies defend multiple nests, and nests with large entrances are harder to defend from intruders, irrespective of the number of soldiers recruited to the entrance [81]. As might be expected, focal groups under high threat of an intergroup contest decrease soldier recruitment to large-entrance nests; this might allow the colony to compete over more easily defendable nests while sacrificing less-defensible nests [81].

Concluding Remarks and Future Perspectives

Intergroup contests are widespread and likely play a key role in both the evolution of social living and the distributions of groups and the resources they use. In the same way as for dyadic

Outstanding Questions

To what extent do self- and mutual assessment models, and models of human military and economic conflict, apply to intergroup contests in other social organisms?

At what level is intergroup contest assessment carried out? Do group members assess themselves and/or opposing members independently, or does the whole group unite in coordinated assessment?

How diverse are intergroup contest assessment strategies, and what are the correlates of this diversity? Most research to date has focused on non-human primates; studying a wider array of social-living organisms will reveal shared principles as well as differences. For example, social organization across taxa may co-vary with assessment strategy.

What is the relative importance of group- versus individual-level traits in determining group RHP?

What levels of contest-relevant heterogeneity exist within groups, and how does heterogeneity affect group-level competitive behaviors and outcomes?

How, and how efficiently, is information on ability and resources communicated among group members? Models of information flow combined with individual tracking techniques can help to test this question.

How does selection in the context of intergroup contests act on the evolution of social traits? Tests at both macroevolutionary and population levels (e.g., via population genetics) will be useful.

What is the interplay between intergroup contests and social evolution theory? How do concepts such as kinship, reproductive skew, and dominance inheritance within groups factor into assessment strategies used during intergroup contests?

What are the causal links between intergroup contests and resource ecology? For example, how are patterns of resource distribution affected by variation in the RHP of competing groups?

> **Box 3. Models from Economics and Interstate Warfare**
>
> Several contest models have been developed in the human economics and interstate warfare literature. Although these models illuminate the dynamics of intergroup contests, they usually model contests between dyads, for example, between individual competitors in an economic game or leaders of nations.
>
> Economic 'dynamic contest' models use game theory to ask how behaviors change according to the efforts expended in a contest and the (expected) payoffs of winning or losing [97]. These models do not explicitly incorporate assessment – that is, the contest is not modeled as an information-gathering process – but assessment is implied because effort levels change based on costs and payoffs. An outcome of dynamic contest models relevant to assessment is the 'discouragement effect' [98]: if the effort required to win a contest exceeds the payoff of success, competitors should stop competing. This is broadly similar to a 'giving-up decision' in dyadic assessment models, in which a competitor gathers enough information on (their own and/or opponent) resource holding potential (RHP) to decide to give up the fight. In dynamic contest models, both parties can experience a discouragement effect, leading to a two-sided peace [98] similar to 'dear enemy' effects in territorial groups [99]. Dynamic contest models appreciate a variety of contest forms, including tug-of-war contests, races, tournaments, and repeated incumbency contests [97].
>
> Models of interstate warfare have explicitly considered the assessment of ability. Fearon [100] argued that, if the leaders of nations had perfect information on relative strength, they should resolve conflicts without war. Only with imperfect information on ability, or if nations are incentivized to conceal information on ability, should warfare result as a means gathering this information. This insight led to 'costly process' models of warfare in which (i) the conflict itself facilitates assessment of relative ability, (ii) nations can return to the bargaining table, and (iii) warfare ceases when the opponent's ability to continue competing, or to inflict costs, is accurately assessed ([101–103], reviewed in [104]). Costly process models have been related to dyadic assessment models [105].
>
> Rusch and Gavrilets [13] review intergroup conflict models (some based on the economics literature) with more than two players. These models ask how the frequency of, and individual and group-level efforts during, intergroup contests are affected by within-group heterogeneity in payoffs and costs. However, as Rusch and Gavrilets [13] note, n-player models that explicitly consider assessment (e.g., of relative RHP) during intergroup contests are rare.

What role do intergroup contests play in regulating animal populations? Can studies of intergroup contests inform conservation research?

contests, research into assessment during intergroup contests can link RHP, the ownership and value of resources, and experience with the decisions groups make during contests.

Future work on intergroup contests will benefit from connections between theory and experiment similar to those that are fundamental to the dyadic contest assessment framework (see Outstanding Questions). For example, game-theoretical models of assessment strategies during intergroup contests, as well as adaptations of human warfare and economic models (Box 3), can be validated and expanded upon by experimental tests and field-based observations. There is also exciting scope for testing how the unique challenges of group living (e.g., heterogeneity and social cohesion, Box 2) affect assessment strategies. Studies of intergroup conflict may also inform ecology and conservation; for example, if intergroup conflict acts to limit population densities (e.g., [61]). Combined with our strong knowledge from dyadic contests, a focus on intergroup contest assessment can lead to a united understanding of how animals gather and use information during contests.

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