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The logic of animal intergroup conflict: A review

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ABSTRACT

We review the literature on various approaches to modeling animal intergroup conflict behavior in theoretical biology, highlight the intricacies emerging in the process of adding due biological realism to such models, and point out recent empirical findings that can inspire future theorizing.

1. Introduction

More than two millennia ago, in his *History of Animals*, Aristotle observed that “There is enmity between such animals as dwell in the same localities or subsist on the same food. If the means of subsistence run short, creatures of like kind will fight each other” (Aristotle, 1984, p. 949). In his *On the Origin of Species*, Darwin even limned life itself metaphorically as the ‘struggle for existence’, acknowledging that all forms of life are inevitably entangled in conflicts (Darwin, 1859). While the horrible events of the first half of the 20th century temporarily led to a focus of prominent European biologists on the more peaceful sides of animal behavior (Lorenz, 1963; Tinbergen, 1968), the modern synthesis in evolutionary biology (Huxley, 1942), with its emphasis on the ‘egoistic gene’ (Dawkins, 1976), has continuously upheld conflict as one of the most important themes in biology. Thus, it might not be a coincidence that the development of evolutionary game theory and its subsequent success in theoretical biology, economics and other disciplines began with a groundbreaking paper on ‘the logic of animal conflict’ (Maynard Smith and Price, 1973).

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Conflicts between forms of (pre-)life, be they viruses, unicellular organisms, or more complex living beings, arise when one interferes in some way with another's structural integrity, resource supply, growth, dispersal or reproductive interests. Obviously, such a broad definition of conflict comprises not only direct conflicts in which at least one party actively seeks to harm the other, but also indirect conflicts in which parties are negatively affected by each other's mere existence or proliferation. Well-known examples of such indirect conflicts are intraspecific evolutionary arms races between trees competing for access to sunlight by growing taller (Dawkins and Krebs, 1979). Examples of direct conflicts, on the other hand, include interspecific predator-prey and host-parasite relations (Barbosa and Castellanos, 2005; Galvani, 2003; Schoener, 1983), chemical warfare between microbe species (Czaran et al., 2002), and intraspecific contests and potentially lethal fights (Enquist and Leimar, 1990), e.g. over reproductive access (Clutton-Brock and Huchard, 2013), parental investment (Trivers, 1974), or territory (Willems et al., 2013).

The central role of both direct and indirect conflicts in the evolution of virtually all forms of life has led to an abundance of respective empirical studies (for overviews see: Hardy and Briffa, 2013; Huntingford and Turner, 1987), and, when conceptualized as 'the struggle for existence', indirect conflict is implicitly present in practically all work in theoretical biology. Compared to this omnipresence of indirect conflict, intraspecific direct conflicts have remained a somewhat peripheral topic. Still, the respective literature has produced a number of seminal models, most of them closely tailored to distinct instances of aggressive behaviors observed in the field (for complementary reviews see: Kokko, 2013; Sherratt and Mesterton-Gibbons, 2013). One likely reason for the comparably high degree of segmentation in the theoretical literature on direct conflicts is that biological theorizing often quickly exchanges ideas and arguments with naturalist field work, as exemplified by the observational studies on non-lethal stag fights in deer that inspired Maynard Smith and Price's models (Maynard Smith, 1974; Maynard Smith and Parker, 1976; Maynard Smith and Price, 1973), and vice versa (Clutton-Brock et al., 1979). The concentration of theoretical work in biology on select phenomena resulting from this close interplay of field and desk work, as well as the need for theories to remain testable by empiricists (Fawcett and Higginson, 2012), may thus have led to the current array of relatively specialized theories on animal conflict behavior.

The aim of this review is to present a structured overview of the existing theoretical literature on intergroup conflict behavior in biology. In doing so, we draw on instructive works by colleagues from theoretical biology and economics (Dechenaux et al., 2015; Kokko, 2013; Sheremeta, 2015; Sherratt and Mesterton-Gibbons, 2013). We follow their 'top-down' approaches of organizing their overviews according to general models of the incentive structures potentially faced by competing individuals and groups. Consistent with most biological models of conflict behavior, we use game theoretical terminology (Broom and Rychtar, 2013; Brown, 2016; Maynard Smith, 1982; for an alternative modeling approach see, e.g.: Santarlasci et al., 2014).

Two earlier, highly informative overviews of approaches to modeling animal conflict behavior already exist (Kokko, 2013; Sherratt and Mesterton-Gibbons, 2013). However, these mainly focus on dyadic and triadic conflict models. We complement them here by putting special emphasis on models of intergroup conflicts.

Inevitably, our review cannot do justice to the vast body of empirical literature on animal conflict behavior (for overviews of this literature see: Hardy and Briffa, 2013; Huntingford and Turner, 1987). Additionally, although we include several methodologically instructive models tailored to ancestral human intergroup conflicts, we confine this review mostly to the study of non-human animal behavior (for comprehensive reviews of human intergroup conflict behavior see, e.g., Glowacki et al. (forthcoming); Böhm et al. (forthcoming); as well as the other papers collected in this issue; Keeley, 1996; and Gat, 2008). Thus, we hope that our review will be found useful by an interdisciplinary readership interested in theoretical insights into the logic and dynamics of animal conflict and also by theorists looking for a guide to the respective methodological toolbox used by theoretical biologists.

2. Approaches to modeling intergroup conflict in biology

As the classic Hawk-Dove game introduced by Maynard Smith and Price (1973) set the stage for the majority of subsequent theoretical approaches to studying conflict in biology, we will start out by briefly recapitulating its main characteristics. Subsequently, we will extend our formalization of the game to be applicable to intergroup conflicts and use this extended version of the game to structure our review of different modeling approaches to animal intergroup conflict behavior and dynamics.

In the canonical Hawk-Dove game, a population of individuals is engaged in dyadic conflicts over an indivisible resource of value B. Individuals can express two different types of conflict behavior, i.e. strategies: Hawk and Dove. Hawks unconditionally escalate while Doves shy away from any conflict. Thus, if a Hawk meets a Dove, the Hawk wins the resource with certainty and free of cost, payoff B, while the Dove gains nothing but also avoids the costs of an escalated fight, payoff 0. If two Doves meet, on the other hand, chance determines which one of the two shies away first, resulting in an expected payoff of $B/2$ each. Finally, if two Hawks meet, both escalate and incur a cost C if they lose the fight, which is usually assumed to be greater than the value of the resource, i.e. $C > B$. The winner of this escalated fight is again determined randomly, leaving each Hawk with an expected payoff of $(B - C)/2$. The resulting payoff matrix is shown in Table 1.

As can easily be seen from Table 1, the Hawk-Dove game has no Nash-equilibria in pure strategies as long as $C > B$. While Hawks always beat Doves, their unconditional strategy of always escalating when fighting each other comes with high costs. Thus, if there are many Hawks, so that fights between them occur frequently, Hawks actually fare worse on average compared to Doves.

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Table 1
Payoff matrix of the symmetrical Hawk-Dove game (for a more thorough motivation see, e.g., Mesterton-Gibbons, 1992); only row-player payoffs are shown; B represents the value of the contested resource; C represents the cost incurred by a player when engaged in an escalated fight; a standard assumption is that $C > B$.

	Hawk	Dove
Hawk	$(B–C)/2$	B
Dove	0	$B/2$

Maynard Smith and Price interpreted the game shown in Table 1 as representing expected life-time fitness outcomes for animals pursuing genetically fixed strategies and asked the crucial question: how will the composition of a population of such animals change over time, if higher payoffs in the stage game lead to greater reproductive success for the respective strategy? This led them to the development of one of the central concepts of evolutionary game theory, the ‘evolutionarily stable strategy’ (ESS; Maynard Smith, 1972, 1982), which characterizes a special class of Nash-equilibria. An ESS is a strategy that, once it is sufficiently common in a population, cannot be invaded by sufficiently rare alternative strategies. Formally, when a population consists of shares ε and $(1-\varepsilon)$ of individuals pursuing strategies j and i, respectively, then i is an ESS if, for a sufficiently small ε,

$$(1-\varepsilon)\cdot\pi_{i,i}+\varepsilon\cdot\pi_{i,j} > (1-\varepsilon)\cdot\pi_{j,i}+\varepsilon\cdot\pi_{j,j},$$

where $\pi_{a,b}$ denotes the expected payoff to strategy a when playing against strategy b and ε represents the so called ‘invasion threshold’ (see, e.g., Gintis, 2009). In many games, equilibria defined by ESS can be interpreted as representing mixed states of the population (see, e.g., Bergstrom and Godfrey-Smith, 1998; Gintis, 2009). In the Hawk-Dove game, for example, a mixed ESS equilibrium is given by a population consisting of proportions of B/C hawks and $(1-B/C)$ doves.

Two implications of this early central insight are particularly important. One, the evolutionary dynamics of conflicts over resources in animals do not necessarily distinguish a unique winner: aggressive (Hawk) and conflict avoiding (Dove) strategies can co-exist stably, at least theoretically. Second, empirical observations of both aggressive and peaceful behavior within or between species cannot be taken to imply that the conflict between the respective behavioral strategies is undecided as yet, as the co-occurrence of peaceful and aggressive behavior does not necessarily represent an off-equilibrium state of the population. It could also be that natural selection is continually stabilizing the particular mix of behavioral strategies being observed.

To link the classical Hawk-Dove model just discussed with models of intergroup conflict, let us rewrite the former using alternative notation. Let $x_i \in \{0, 1\}$ specify the fighting effort of individual i in a dyadic conflict, with $x_i = 0$ representing the Dove strategy and $x_i = 1$ representing the Hawk strategy. Then, the expected payoff of using strategy x_i can then be written as

$$\pi_i = P_i\cdot B-(1-P_i)\cdot C\cdot x_i,$$

where P_i gives the probability of individual i winning the conflict, which naturally depends on the strategy x_j used by the opponent. Consistent with the assumptions of the Hawk-Dove game, P_i can be defined as

$$P_i = \begin{cases} \dfrac{x_i}{x_i+x_j}, & if\ x_i+x_j>0 \\ \dfrac{1}{2}, & if\ x_i=x_j=0 \end{cases},$$

a function well known in the economics literature as the *Tullock contest success function* (Tullock, 1980). As above, the population is predicted to evolve to a state where the frequency of Hawks is B/C, implying that the average fighting effort in the population is $\bar{x} = B/C$ in equilibrium.

From this minor reformulation of the dyadic Hawk-Dove game, it is only a small step to a simple model of intergroup conflict.

2.1. A simple model of animal intergroup conflict

Let us start by assuming the meta-population consists of G subgroups, each consisting of n individuals. These groups are engaged in pairwise conflicts over resources of value B. Let variable $x_{ik} \geq 0$ specify the effort of individual i in group k towards group success. Efforts of group members are then aggregated into a group effort X_k. Following the economics literature, we call the function combining individual efforts into group effort the *impact function*. The most common impact function in the literature is linear, i.e. $X_k = \sum_i x_{ik}$, and simply adds up the fighting efforts of all individuals in group k. Given group efforts

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X_k and X_l, we can then define the *group contest success function*, which specifies the probability that group k wins a contest with group l, for example as

$$P_k = \begin{cases} \dfrac{X_k}{X_k + X_l}, & \text{if } X_k + X_l > 0 \\ \dfrac{1}{2}, & \text{if } X_k = X_l = 0 \end{cases}$$

P_k is a straightforward generalization of the Tullock contest function used for describing contests between individuals (Konrad, 2009; Tullock, 1980). Let us assume further that costs to participating individuals, c, accumulate linearly with effort, independent of the contest's outcome, and that individual i in group k obtains the share v_{ik} of B in the event group k wins. Then, the expected payoff to individual i in group k can be written as

$$\pi_{ik} = P_k \cdot (v_{ik} \cdot B) - c \cdot x_{ik}.$$

Note that this payoff structure still is quite similar to that of the Hawk-Dove game. One central difference is that the costs of conflict are paid by all participants, rather than just by the loser. Consequently, for the special case of $n = v_{ik} = 1$ our model reduces to a variant of the Hawk-Dove game that only differs from the original in that fighting efforts always entail costs, irrespective of the conflict outcome. These increased costs are also reflected in the equilibrium effort, which in this case is $x^* = B/4c$.

Another crucial difference is the term v_{ik} determining the share of B going to individual i when group k wins. For example, $v_{ik} = 1/n$ if everyone in group k receives an equal share. The set of values $v_{1k}, \ldots, v_{nk}$, specifies the *sharing rule* in group k. It must be noted that this sharing rule marks a significant difference between the logic of dyadic contests and the logic of intergroup conflicts: if v_{ik} does not depend on the costly individual effort x_{ik}, for example, there is an incentive to reduce or even completely withdraw effort for individual i. As a result, the group then faces a *collective action problem* which can undermine within-group cooperation (Hardin, 1968; Olson, 1965). Overcoming such collective action problems is a general problem that complicates not only the mobilization of fighting efforts in intergroup conflicts, but also many other group activities–in human societies as well as in other social animals (Gavrilets, 2015; Gavrilets and Fortunato, 2014; Willems and van Schaik, 2015).

In the following we will consider a number of specific models of voluntary participation in intergroup conflict and identify individual or group efforts predicted to emerge at evolutionarily stable equilibria. This focus on voluntary contributions and ESS is due to the fact that this perspective is widely considered to be the most appropriate for describing the outcomes of natural selection on behavioral traits in non-human animals. Additional factors such as institutionalized sanctioning or redistribution systems, or rational thinking and foresight, must obviously not be disregarded in analyses of human behavior. Yet, they can be largely neglected in the non-human context (but see Section 4.3 for conflict-related rewards and punishments). In contrast, biologically and evolutionarily relevant factors such as random genetic drift, genetic relatedness or group selection are often neglected in models of contemporary human behavior, but will be of significant importance here.

The simple model just outlined can be modified and generalized in various ways, facilitating insights into the basic logic of animal intergroup conflict. Furthermore, when the aim of the modeling process is to retain a sufficient level of biological realism, additional assumptions about population structure, group formation and strategy propagation must be introduced. However, as such additional assumptions are crucial for every model in theoretical biology, we will examine different mathematical extensions and modifications of the simple model first (Sections 2.2–2.4). Thereafter, we move on to discuss how including different biological structural conditions, such as population size, demography or genetic relatedness, affects models of intergroup conflict (Section 3). An overview and a rough classification of selected models published in recent years can be found in Table 2. Table S1 collects more than 220 complementary references.

2.2. Winning and losing: ways of modeling contest success and costs

The group contest success function, P_k, introduced above implies that the group exerting the greater aggregate effort is more likely to win the conflict, with $P_k \to 1$ when $X_k/X_l \to \infty$. Provided the difference in group efforts is sufficiently small, the outcome of such a conflict represents a lottery in which the inferior group still maintains a considerable chance of winning. However, the assumption of such a probabilistic nature of the conflict outcome is not always justified. For conflicts in which the difference in fighting efforts of the two parties is more decisive, P_k can be generalized to

$$P_{k,\beta} = \frac{X_k^\beta}{X_k^\beta + X_l^\beta}.$$

Here, the added parameter $\beta \geq 0$ determines the decisiveness of a conflict in the following way: for small β, i.e. $\beta \to 0$, differences in efforts cease to matter for conflict outcome, which becomes perfectly random in the limiting case of $\beta = 0$. For large β, on the other hand, i.e. $\beta \to \infty$, stochasticity ceases to matter and small differences in efforts become decisive. Models using this type of generalized contest success function are used frequently in theoretical biology, where contest models with

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Table 2
Overview and rough classification of selected models of animal conflict behavior in theoretical biology from recent years (2007–2016).

Study	Population size and grouping	Demographics	Conflict	Sharing	Methods	Specific notes
Barker et al. (2016)	$N = \infty$; $G < N$	$R+$, M^{R}, P^{R}	O^{X}, S^{W}	$V^{\neq}$	A^{A}, D^{S}	Heterogeneous fighting capabilities
Biernaskie and Foster (2016)	$N = \infty$; $G < N$	$R+$, M^{R}, P^{R}	$O^{X\#}$, S^{W}	$V^{\neq}$	A^{A}, D^{S}	Empirically tested
Kaiping et al. (2016)	$N < \infty$; $G < N$	$R-$, $M^{\#}$, $P^{\#}$	O^{X}, S^{T}	$V^{\neq}$	A^{S}, D^{D}	Fitness-based migration considered
Mesterton-Gibbons and Sherratt (2016)	$N = \infty$; $G = N$	$R-$, $M-$, $P-$	O^{X}, S^{O}	$V-$	A^{A}, D^{S}	Resource valued asymmetrically
Pandit et al. (2016)	$N < \infty$; $G < N$	$R-$, $M-$, $P-$	O^{N}, S^{T} $(\beta = \infty)$	$V^{\neq}$	A^{A}, D^{S}	Heterogeneous fighting capabilities
Zhang and Perc (2016)	$N < \infty$; $G \ll N$	$R-$, M^{*}, $P^{\ddagger}$	$O^{X\#}$, S^{T}	$V^{=}$	A^{S}, D^{D}	
Gavrilets and Fortunato (2014)	$N \leq \infty$; $G < N$	$R+$, $M^{\#}$, $P^{\ddagger}$	O^{X}, S^{T}	$V^{\neq}$ & $V^{=}$	A^{A} & A^{S}, D^{S} & D^{D}	
Konrad and Morath (2014)	$N < \infty$; $G = N$	$R-$, $M-$, $P-$	O^{N}, S^{W}	$V-$	A^{A}, D^{S}	
Rusch (2014b)	$N < \infty$; $G \ll N$	$R-$, M^{*}, $P^{\dagger}$	$O^{N\#}$, S^{T}	V^{P}	A^{S}, D^{D}	Attack and defense separated
Konrad and Morath (2012)	$N < \infty$; $G < N$	$R-$, M^{∞}, $P-$	O^{X}, S^{T} $(\beta = 1)$	$V^{\neq}$	A^{A}, D^{S}	ESS includes generic sharing rule
García and van den Bergh (2011)	$N < \infty$; $G \ll N$	$R-$, M^{*}, $P^{\ddagger}$	$O^{X\#}$, S^{T}	$V^{=}$	A^{S}, D^{D}	
Lehmann (2011)	$N = \infty$; $G < N$	$R+$, M^{*}, $P^{\#}$	$O^{N\#}$, S^{T}	$V^{=}$	A^{A}, D^{S}	
Bowles (2009)	$N = \infty$; $G < N$	$R+$, M^{R}, $P^{\ddagger}$	$O^{X\#}$, S^{T} $(\beta = \infty)$	$V^{=}$	A^{A}, D^{S}	Empirical calibration of conflict rates and relatedness
Lehmann and Feldman (2008)	$N = \infty$; $G < N$	$R+$, M^{*}, $P^{\dagger}$	O^{X}, S^{T}	$V^{=}$	A^{A}, D^{S}	Sexes separated, two-locus model
Choi and Bowles (2007)	$N < \infty$; $G \ll N$	$R-$, $M^{\#}$, $P^{\#}$	O^{N}, S^{T} $(\beta = \infty)$	$V^{=}$	A^{S}, D^{D}	
Reeve and Hölldobler (2007)	$N = \infty$; $G < N$	$R+$, M^{R}, P^{R}	O^{X}, S^{W}	$V^{\neq}$	A^{A}, D^{S}	

Symbols used

Pop. size and grouping	'$N < \infty$' ~ finite population model; '$N = \infty$' ~ infinite population model; '$N \leq \infty$' ~ both variants considered; '$G = N$' ~ groups modeled as a single player; '$G < N$' ~ groups modeled as multiple players; '$G \ll N$' ~ as $G < N$, but with particularly small groups
Demographics (relatedness, migration & repopulation)	'R^{+}' ~ relatedness modeled explicitly; '$R-$' ~ relatedness not modeled; '$M-$' ~ no migration modeled; 'M^{R}' ~ migration modeled through relatedness; 'M^{*}' ~ multiple migration levels considered; '$M^{\#}$' ~ multiple migration scenarios considered; 'M^{∞}' ~ random regrouping in each generation; '$P^{\ddagger}$' ~ whole groups are replaced; '$P^{\dagger}$' ~ groups are partially repopulated; 'P^{R}' ~ repopulation modeled through relatedness; '$P^{\#}$' ~ multiple repopulation scenarios considered; '$P-$' ~ repopulation not modeled
Conflict (occurrence & intensity, success function)	'O^{N}' ~ conflict occurrence determined endogenously; '$O^{N\#}$' ~ as 'O^{N}', but multiple scenarios considered; 'O^{X}' ~ conflict occurrence determined exogenously; 'O^{X*}' ~ as '$O^{X\#}$', but multiple scenarios considered; 'S^{W}' ~ Tug-of-war-type success function; 'S^{T}' ~ Tullock-type success function [if available, β is stated in brackets]; 'S^{O}' ~ other success function
Sharing	'$V^{=}$' ~ equal sharing; $V^{\neq}$ ~ potentially unequal sharing; 'V^{P}' ~ proportional sharing rule; '$V-$' ~ sharing not modeled
Methods	'A^{S}' ~ simulations; 'A^{A}' ~ analytical solutions; 'D^{S}' ~ static analyses; 'D^{D}' ~ dynamic analyses

$\beta = \infty$ are known as 'wars of attrition' (Bishop and Cannings, 1978; Chatterjee et al., 2012; Maynard Smith, 1974). Introducing $P_{k,\beta}$ to our simple model and assuming equal sharing within all groups, i.e. $v_{ik} = 1/n$, we obtain

$$X^{*} = \frac{b}{2c} \cdot \frac{n \cdot \beta}{n + \beta - 1}$$

as the total group effort in equilibrium (Konrad, 2009); herein $b = B/(2 \cdot n)$ is shorthand notation for the share of the resource going to an individual if the resource were divided equally between competing groups. Increasing the decisiveness parameter β thus increases the equilibrium efforts exerted by groups in our model.

Two other assumptions of our simple model are that the contested resource (i) is indivisible, and can thus eventually be obtained by only one of the competing parties, and (ii) does not change its value with group efforts. Changing the first assumption only requires a reinterpretation of the contest success function as representing the share of the resource being obtained by each party after the conflict, instead of representing a winning probability (as, e.g., in Gavrilets and Fortunato, 2014). Relaxing the second assumption, however, requires a slight reformulation of the model, for example to

$$\pi_{ik} = P_k \cdot (v_{ik} \cdot B \cdot [1 - X_k - X_l]).$$

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Here, efforts X_k and X_l are measured in proportion to the available resource B and contest costs are modeled as a reduction of the value of the contested resource proportional to the exerted efforts. Models of this type are known as ‘tug of war’ games. These have been frequently applied in the study of dyadic conflict over reproduction within groups (Reeve et al., 1998; Reeve and Shen, 2006; Shen and Reeve, 2010), but have also been generalized to full-scale between-group conflicts more recently (Reeve and Hölldobler, 2007; for an analogous modeling approach in economics see, e.g., Smith et al., 2014).

Finally, other modifications of the simple model take into account that contest costs might not be a linear function of effort, but instead might depend on differences in effort and individual fighting capabilities in a non-linear fashion. The same holds for the impact function: it obviously need not be the case that aggregate group efforts are best captured as the simple sum of individual efforts. Instead, deviations from this assumption in both directions can be motivated, as greater efforts, e.g., might be harder to coordinate but might also allow for more efficient fight tactics based on a division of ‘labor’. It has recently been shown that introducing nonlinear cost or impact functions to a model similar to our illustrative simple model, leads to all individuals contributing to collective efforts in equilibrium, even in groups with non-egalitarian sharing rules (Gavrilets, 2015).

Another prominent class of intergroup conflict models has also explored several such non-linear relations. For example, if we let α_k and α_l denote the per capita fighting capabilities in groups k and l and interpret X_k and X_l as the numbers of group members participating in the fight at a time t, then group l can impose a loss of $-\alpha_l \cdot X_l$ on group k per unit of time that the fight continues and, vice versa, group k can damage group l at a rate of $-\alpha_k \cdot X_k$. Rewritten as differential equations, we get $dX_k/dt = -\alpha_l \cdot X_l$ and $dX_l/dt = -\alpha_k \cdot X_k$. It can be shown that a fully escalated fight of this type is won by group k if $\alpha_k \cdot K^2 > \alpha_l \cdot L^2$. In this condition, known as Lanchester’s square law (Lanchester, 1916), K and L represent the initial efforts of groups k and l at the outset of the fight. Further, it can be shown that, eventually, $K^* = (K^2 - [\alpha_l/\alpha_k] \cdot L^2)^{1/2}$ combatants of the victorious group, k in this case, survive, while all defeated combatants die, i.e. $L^* = 0$. Models of this ‘Lanchester-type’ thus take into account that both differences in per capita fighting capability and the numerical strength of the parties might non-linearly affect contest outcomes (see, e.g., Adams and Mesterton-Gibbons, 2003; Johnson and MacKay, 2015; for discussions and further extensions). So far, however, this approach has not been explored within a game-theoretic formalism.

2.3. Sharing and equality: modeling heterogeneity

Apart from the way in which differences in aggregate efforts X_k and X_l between groups are assumed to influence conflict outcomes, two other crucial components of conflict models are the sharing rule, v_{ik}, and the range of effort levels available to group members, x_{ik}. The assumptions that (i) benefits are distributed equally within groups, i.e. $v_{ik} = 1/n$, (ii) marginal costs, c, are the same for all individuals, and (iii) individuals do not differ in the range of effort levels available to them, i.e. $0 \le x_{ik} \le e$ for all i and k, substantially facilitate analyses in many cases. They are unlikely to hold for many social animals, however, including humans. Often, it is more appropriate, for example, to assume that individuals differ in social rank, i.e. in their rights to access their group’s resources, in their marginal costs, and in their abilities, i.e. $0 \le x_{ik} \le e_{ik}$, where e_{ik} depends on both i and k. Furthermore, it is often more realistic to assume that rank and ability are interrelated, e.g. by letting v_{ik} be a positive function of e_{ik}.

Introducing such within-group variation, of course, induces interests of group members that are not necessarily aligned, for example when a number of privileged individuals benefit much more from a victory than their fellow group members. Such potential conflicts of interest within groups can, in turn, undermine group-level cooperation, which is needed for success in competition with other groups. Although such heterogeneity can therefore be expected to have significant effects in the evolution of conflict behavior, it has largely been neglected in existing formal theories of intergroup conflict. Noteworthy exceptions in the recent literature include the following: Konrad and Morath (2012) assume equal individual abilities, but derive evolutionarily stable strategies in a tug-of-war type conflict that are a function of a generic sharing rule; Gavrilets and Fortunato (2014) study the effects of unequal sharing rules and heterogeneity of individual abilities and marginal costs by means of systematic numerical simulation; Rusch (2014b) assumes shares v_{ik} to be a positive function of efforts x_{ik} in a simulation model; and Pandit et al. (2016) analyze the probability of occurrences of conflicts between groups characterized by heterogeneous fighting abilities and unequal sharing rules.

These works only represent first steps toward a more comprehensive understanding of the effects of different types of heterogeneity in the evolution of between-group conflict behavior. Still, they already allow for remarkable observations. In Pandit et al.’s model, e.g., higher variances of fighting abilities within groups lead to higher probabilities of between-group aggression. Gavrilets and Fortunato find that under conditions of strong between-group competition, dominant individuals who usurp a significant share of the group’s resources are predicted to effectively sacrifice themselves for their group in conflicts. Yet, these studies also show that the effects of heterogeneity depend sensitively on specific additional assumptions made in the respective models (for a first review of collective action models in biology allowing for heterogeneity see: Gavrilets, 2015).

Using an approach as in Gavrilets (2015), introducing heterogeneity in v_{ik} to our illustrative model yields the following result. Equilibrium group effort is predicted to amount to $X^* = \frac{b}{2c}$ in the case $v_{ik} = 1/n$. However, when all v_{ik} are different, only that individual within each group who has the largest stake v_{ik} in her group’s success, $v_{\max,k}$, will exert a positive effort, while all other individuals will free-ride contributing nothing (also see Baik, 1993). Then, assuming for simplicity that

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$v_{\max,k} = v_{\max}$ in all groups, the equilibrium contributions are $x^*_{\max,k} = v_{\max} \cdot \frac{b}{2c}$. Thus, full heterogeneity in v_{ik} is predicted to have the effect of lowering overall conflict efforts, as long as $v_{\max} < 1$.

2.4. Why fight? Conflict escalation and avoidance

Another point considered infrequently in theoretical analyses of intergroup conflict behavior is the question of whether it is ultimately beneficial to engage in conflicts at all. The majority of models in the literature either focuses on determining optimal strategies of individuals already involved in a specific type of conflict or assumes that conflicts between groups occur randomly with an exogenously fixed probability. Just like the classic Hawk-Dove game explicitly does, these models implicitly identify peacefulness with the absence of a willingness to invest into a group's conflict efforts, i.e. $x_{ik} = 0$. This equation makes peacefulness and free-riding indistinguishable, although these might be quite different strategies (also see Robinson and Barker, 2017). In addition, the common simplifying assumption of exogenously determined conflict occurrence makes it impossible for such models to study how more peaceful groups fare in comparison to more aggressive ones when groups can actively avoid conflict escalation (for a model tackling a similar issue in the context of within-group cooperation without between-group conflict see, e.g., Brandt et al., 2006).

While modeling intergroup conflict occurrence as exogenously determined can be deemed conventional, there currently is no standard approach for relaxing this assumption, as the few papers that do so tackle this problem in rather distinct ways. For example, Choi and Bowles (2007) and Rusch (2014b) each let conflict occurrence between groups be determined endogenously in their simulations. Choi and Bowles use a probabilistic function, which increases with the difference in the number of individuals willing to engage in conflict on each side. A comparable approach is taken by Lehmann (2011) in his analytical models, which also use a probabilistic conflict occurrence function. Rusch (2014b), on the other hand, includes an endogenously evolving individual 'aggressiveness' trait in his simulation model and lets group A attack group B deterministically if the difference in strengths between the two groups is larger than the average aggressiveness threshold of the individuals in group A.

Using formally markedly different approaches, Pandit et al. (2016) focus on studying conflict occurrence probabilities between groups of varying sizes and sharing rules in a model tailored to the ecologies of mobile hunter-gatherer bands and chimpanzees. Hamelin and Lewis (2010) present a spatial model to predict the formation of buffer-zones between hostile packs of wolves. Konrad and Morath (2014) take yet another very different approach and study a two stage game, in which groups bargain over the division of a resource first and only aggress each other if no mutually agreeable division can be found peacefully.

It is quite interesting to note that active avoidance of conflict escalation is understudied in the current theoretical literature on intergroup contests in animals, mainly for two reasons. First, many overviews of aggressive behavior in animals eventually reach the conclusion that full-blown intergroup conflicts only occur in relatively few species (e.g., Wrangham, 1999). The current theoretical literature, thus, does not answer the important question of why this is the case. Second, in the literature on dyadic animal conflicts, refined models of conflict avoidance strategies were developed soon after Maynard Smith and Price's seminal contribution (e.g. Enquist and Leimar, 1983; Maynard Smith and Parker, 1976). Many factors leading to reduced conflict levels received intense theoretical and empirical attention (but also see Enquist and Leimar, 1990). For example, such factors include strategies allowing for the assessment of one's own and/or opponent strength prior to conflict escalation (reviewed in Kokko, 2013), and so called 'winner and loser effects' (reviewed in Rutte et al., 2006). The latter is the use of information about one's own and opponent's performance in previous conflicts in the decision whether or not to escalate. Hence, with respect to active conflict avoidance, the literature on dyadic conflicts offers a plethora of inspirations for future work on intergroup conflicts in animals.

3. Adding further biological realism

The potential extensions of intergroup conflict models outlined in Section 2 of course do not exhaust the set of factors potentially relevant in modeling animal conflict behavior, as they are limited to changes in assumptions about individuals' characteristics and the strategic features of the conflicts in which they are engaged. Consequently, let us now turn to reviewing selected approaches for studying the evolutionary dynamics and modeling the structure of populations in which these conflicts occur. As stated above, many of these approaches are of general importance in theoretical biology. In models of intergroup conflict, however, they gain additional importance, particularly because the outcome of such conflicts is often assumed to have direct consequences for a population's composition, bypassing the more gradual changes of the population resulting from natural selection. To start, let us define more accurately the currency in which the gains and losses potentially resulting from animal intergroup conflicts are paid, i.e. the unit of measurement of π_{ik}.

3.1. Fitness and strategy evolution

Evolutionary biologists conventionally conceptualize the struggle for existence as a struggle for successful reproduction, which of course requires survival up to at least the age of propagation, and for many species even longer (Stearns, 1992). Accordingly, 'payoffs' in evolutionary game theory are usually thought of as modeling benefits gained and losses incurred

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that eventually affect the reproductive success of individuals, i.e. their (Darwinian) fitness. An important distinction must be made, however, between static models of fitness maximization and dynamic models of population evolution (see, e.g., Broom and Rychtar, 2013; Hofbauer and Sigmund, 1998). Static models analyze how well a particular strategy performs in comparison to a set of competing alternative strategies in a given game. One way of carrying out such a static analysis is the identification of ESS (see Section 2 above). Dynamic models, on the other hand, analyze how the composition of a population consisting of individuals pursuing competing strategies changes as a consequence of the respective strategies' performance. In most cases, this depends on the frequency distribution of all strategies in the population.

The first step in describing such evolutionary dynamics is to specify exactly how strategies change over time. Three such 'strategy revision protocols' are common: random mutation, adaptive social learning, and myopic optimization (see, e.g., Sandholm, 2011). In the first case, it is commonly assumed that individual strategies are encoded genetically and are changed by random mutation and recombination during reproduction. Importantly, if strategies are assumed to be controlled genetically, the effects of recombination and epistasis on strategy revision also need to be specified. In the second case, adaptive social learning, an individual randomly picks a group-mate and copies its strategy with a certain probability if that strategy provides a higher payoff. In the third case, myopic optimization, the individual evaluates the payoff consequences of changing its own strategy on the assumption that everybody else keeps their strategies. Then, the individual picks the strategy expected to yield the highest predicted payoff, subject to random errors. Which of these protocols is most suitable depends on the behavioral flexibility and social learning abilities of the species in question.

Once a strategy revision protocol is specified, the study of dynamic models then goes beyond static analyses by asking whether the equilibria defined by ESS, as well as other types of equilibria, can be reached at all, and if so, from which initial compositions of a population and how quickly. Answers to these types of question can, for example, be given in terms of 'basins of attraction' and 'evolutionary trajectories', i.e. by identifying the compositions from which a population gradually converges toward a given equilibrium over time and the route the population takes through its state space to get there.

Over the last four decades, important theoretical insights that directly apply to understanding animal conflict behavior have been gained from the analyses of both static and dynamic models. A general conclusion from these works is that the predictions derived from game theoretical models of the evolutionary dynamics of animal behavior sensitively depend on a priori assumptions about population size, interaction structure and strategy revision protocol. We will not delve into the complexities of dynamic models further here (for overviews see, e.g.: Nowak, 2006a; Sandholm, 2011), but it is important to note at least the following.

A classic approach to population dynamics assumes an infinite meta-population consisting of proportions, ρ_i, of randomly interacting individuals pursuing strategies $i \in \{1, \ldots, m\}$. Furthermore, it assumes ρ_i will change proportionally to the payoff, $\pi_i(\rho)$, that strategy i yields given the current population composition ρ, relative to the current average payoff of all strategies in the population, $\Pi(\rho)$. This results in the well-known replicator equation: $\dot{\rho}_i = \rho_i\,[\pi_i(\rho) - \Pi(\rho)]$, which can be used to identify equilibria by solving for $\dot{\rho}_i = 0$. Note, these equilibria need not be dynamically stable (see, e.g., Zeeman, 1981). While the replicator equation is a key tool in theoretical biology (see Page and Nowak, 2002), its application in understanding animal behavior is limited by its presuppositions of an infinite population whose individuals meet and interact perfectly at random. As will be illustrated in the following Sections (3.2–3.4), altering these biologically unrealistic assumptions, for example by allowing for non-random assortment of individuals, spatial population structuring, or restricting to finite populations, can drastically affect the predicted population dynamics (for further examples see Nowak et al., 2004; Nowak and May, 1992; Sandholm, 2011; Schaffer, 1988).

3.2. *Finite populations*

The arguably most important caveat resulting from these theoretical insights is the following: while strictly dominated strategies are eventually eliminated from a population governed by replicator dynamics (see, e.g., Gintis, 2009), in finite populations every strategy has a certain fixation probability (see, e.g., Lessard, 2005). This means that in finite populations, and particularly under weak selection (Wild and Traulsen, 2007), every strategy has a certain positive probability of eventually growing to dominate the population by random genetic drift, as any strategy in a finite population can become extinct due to chance events that are independent of the performance of the respective strategy itself. This of course complicates the application of finite population models to real animal behavior, as the behavior observed in the field might simply be, to some extent, the result of stochastic events unrelated to the behavioral strategies under study. This is especially true when the impact of the strategies applied by an animal in a certain behavioral domain on its life-time fitness balance is weak, i.e. under weak selection.

A second important result of the study of dynamics of finite populations is that the invasion threshold, ε, of an initially rare mutant can substantially change with meta-population size N. In finite populations, particularly in small ones, ε becomes a function of N, implying that the classical ESS concept no longer represents a suitable criterion for identifying those population compositions that will eventually be stabilized by natural selection. This, in turn, additionally complicates the application of finite-N models, because it requires meta-population size to be tracked thoroughly. For finite-N refinements of the ESS concept see, e.g.: Nowak et al. (2004) and Schaffer (1988).

3.3. Grouping and re-grouping: the importance of demographics

Independent of whether $N=\infty$ or $N<\infty$ is assumed, another biologically crucial modeling choice consists in the questions of how the G subgroups are formed within the meta-population and how stable they are over time. These questions of group formation and stability have received some attention in the literature on dyadic conflicts, particularly in models of alliance formation (Gavrilets et al., 2008; Getty, 1987; Mesterton-Gibbons et al., 2011). These models extend the number of parties involved in a conflict to three and allow for third parties to intervene in a fight. In our notation, however, these models still fall under the category of $n=1$ type approaches, as it depends on individuals' strategies whether or not temporary coalitions are formed. Eventually, groups in these models are unstable, endogenous by-products of individual strategies evolving in potentially all-out competitive populations.

The picture changes, however, for $n>1$ type approaches, in which group membership is introduced as an exogenous factor, i.e. when individuals are modeled as belonging to groups of size two or larger that compete with other such groups. For reasons of feasibility, many of these models assume equally-sized groups composed of individuals that can differ in their strategies but not in other respects (for exceptions see Section 2.3 above and Peña and Nöldeke, 2016). These models show that group size has a crucial effect on the predicted dynamics, so that, for example, within-group cooperation is much easier to establish and maintain if the group size is small (see, e.g., Kaiping et al., 2016). A biologically more realistic scenario, however, is that population sizes and densities have their own dynamics and can experience very rapid changes. In addition, real animal groups split and merge and go extinct. Therefore, explicitly modeling meta-population and subgroup size dynamics and their feedback on a game's structure, i.e. explicitly specifying the 'demographics' of the meta-population, is often a necessary step in achieving both biological realism and relevance. Recent work shows how assumptions about these underlying demographics can substantially alter the predictions that intergroup conflict models yield and how they affect their biological applicability (see, e.g., Kaiping et al., 2016; Lehmann, 2011; Lehmann and Feldman, 2008; Rusch, 2014a).

3.4. Genetic relatedness and group vs. multi-level selection

Another reason why demographics are of such central importance is that while the unit of analysis in most game theoretical models is the individual, the object of natural selection is genes coding for behavioral traits (Abbot et al., 2011; Gardner and West, 2014; Hamilton, 1964). When reproducing, organisms leave progeny who carry a copy of a given gene of their parents with a certain probability r, the so called coefficient of relatedness. Conventionally, r is assumed to approach 1 for clonal reproduction, 0.75 in many eusocial insects (Hughes et al., 2008) and 0.5 for sexual reproduction, but these values can vary depending on the respective likelihood of mutations, inbreeding and other ecological factors.

A fundamental insight of theoretical evolutionary biology is that, by benefitting relatives who carry the same genes, an individual can optimize its fitness balance, even when such behavior causes costs to the target individual (Hamilton, 1964; West et al., 2007). Hamilton's rule, accordingly, states that natural selection will positively select for such behaviors as long as their costs do not exceed their benefits weighted by the probability of sharing the respective genes (Hamilton, 1964; Nowak, 2006b). Thus, not only the *direct fitness* benefits a behavioral trait yields need to be taken into account but also the *indirect fitness* benefits obtained through causing increased reproduction of genetic relatives. This approach to analyzing evolutionary dynamics is known as '*inclusive fitness* theory' (see, e.g., Gardner and West, 2014).

An intergroup conflict model's assumptions about demographics can now affect the relatedness structure within the studied population substantially. In the case of limited dispersal, in which individuals' progeny are more likely to remain in their natal group than leave it, relatedness between the individuals of that group continuously rises and can facilitate the evolution of group-beneficial behaviors, which in that case simply resolve to kin-beneficial behaviors (Ohtsuki, 2010; West et al., 2011). Note, however, that this positive effect of limited dispersal on group-beneficial behavior can be canceled out by the level of within-group competition over reproduction (Kümmerli et al., 2009; West et al., 2001). Moreover, when it is assumed, as for example in (Bowles, 2009; García and van den Bergh, 2011), that groups defeated in conflicts are entirely wiped out and replaced by offspring of members of the victorious groups, such models introduce 'old' group selection *sensu* West et al. (2007), if they do not simultaneously allow for at least some migration of individuals between groups.

While there may be no compelling theoretical arguments against studying evolutionary dynamics under such extreme demographics, the problematic aspect of introducing 'old' group selection mainly lies in the limitations it entails with respect to the application of such models to real animal behavior. After a lively debate in theoretical biology in the last century (Leigh, 2010), 'old' group selection today is thought of as very unlikely to occur in nature, as its main requirement of a very small within-group to between-group competition ratio is unlikely to be met by populations of social animals (also see Biernaskie and Foster, 2016; Langergraber et al., 2011). Instead, many theoretical biologists have adopted the view that more realistic demographics allowing for more variable group memberships are empirically more fruitful.

Although recent years have seen a debate about whether such demographics should be conceptualized as 'inclusive fitness' or 'multi-level selection' models (Lehmann et al., 2007), these types of models are comparable in that they are both based on individual fitness maximization affected by both within-group and between-group competition. Their main difference lies in that the former explicitly track individuals' inclusive fitness, while the latter do not. Which of the two analytical approaches is taken can be considered a matter of mathematical convenience, at least to some extent (West et al., 2008; but see van Veelen, 2009; van Veelen et al., 2012).

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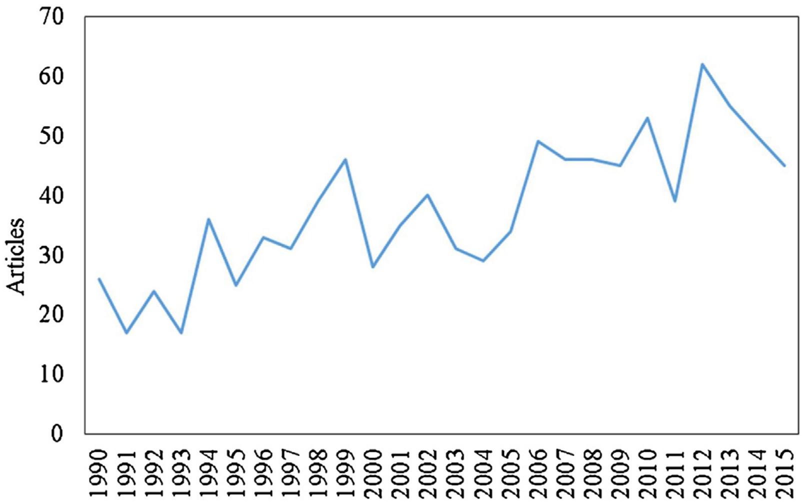

Fig. 1. Conflict-Related Papers in top Biology Journals, 1990–2015.
Note: Fig. 1 displays conflict-related papers that were published in top biology journals between 1990 and 2015. The figure was generated based on five journals (*Animal Behaviour*, *Journal of Theoretical Biology*, *Evolution and Human Behavior*, *Proceedings of the Royal Society B: Biological Sciences*, *Philosophical Transactions of the Royal Society B: Biological Sciences*) and the search terms (fight, conflict, contest, competition, aggress) commonly associated with theories of conflict in biology. Web of Science searches for articles within the given journals with these terms in the title were performed on 29 September 2016.

To illustrate: consider our model from above with $v_{ik} = 1/n$ and assume that average within-group relatedness is equal to r while relatedness between groups is 0. Then, the predicted equilibrium group effort in a one-shot contest between two groups is

$$X^* = \frac{1 + (n-1) \cdot r}{1 + \left(1 - \frac{1}{n}\right) \cdot r} \cdot \frac{b}{c}$$

(Gavrilets and Fortunato, 2014). Increasing relatedness within groups thus increases equilibrium group efforts. Conversely, assume that all individuals have the same degree of relatedness, i.e. within *and* between groups, and introduce group selection by assuming that the contest success function P_k also determines group survival, i.e. assume a two-level Fisher-Wright scheme of individual and group survival (Schonmann et al., 2013). Then, the evolutionarily stable group effort is predicted to be $X^* = \frac{1+b}{c}$. Thus, also in our illustrative model, both group selection and within-group relatedness increase equilibrium efforts.

Reformulating our model in terms of inclusive fitness can be done as follows. In order to obtain the expression that is maximized by natural selection according to inclusive fitness theory, not only do the share of B directly obtained by individual i (i.e. $B \cdot v_{ik}$) and the costs to individual i ($c \cdot x_{ik}$) need to be included in π_{ik}. Instead, the respective shares obtained, and costs incurred, by all of i's relatives as a direct consequence of i's behavior also need to be taken into account, irrespective of which group these relatives belong to. Thus, the expected payoff to individual i in group k becomes,

$$\pi_{ik} = B \cdot \sum\nolimits_k \left(P_k \cdot \sum\nolimits_j r_{ij} \cdot v_{jk} \right) - \sum\nolimits_j r_{ij} \cdot c \cdot x_{ik},$$

where r_{ij} is the coefficient of relatedness between individuals i and j, $r_{ii} = 1$, and k sums over all groups (for models taking similar approaches see, e.g., Ohtsuki, 2010, 2014; Rusch, 2015).

4. Instructive empirical works to inspire future theorizing

As Sections 2 and 3 have shown, the existing theoretical literature on animal intergroup conflicts is diverse. The works discussed above have identified a remarkable variety of assumptions and modeling components that sensitively affect a model's dynamics and long-term predictions, including: (i) impact, (ii) contest success, and (iii) cost functions; (iv) sharing rules; (v) strategy revision protocols; (vi) meta-population and subgroup sizes; (vii) demographics; (viii) within-group heterogeneity; (ix) between-group differences; and (x) genetic relatedness (also see Table 2).

Currently, this diversity largely precludes decisive empirical tests of one model against another, as such tests would require that the models compared differ much less in their fundamental make-up. Still, the richness of the already existing literature indicates at least two things. One, modeling animal intergroup conflict behavior is an intricate but also highly fruitful problem. Second, as the increase in the number of respective models and empirical studies published in recent years shows, it is an increasingly popular topic (see Fig. 1). Nevertheless, at the moment, this branch of the theoretical literature is maybe characterized most fittingly as "still in its infancy" (Sherratt and Mesterton-Gibbons, 2013, p. 43).

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We will highlight what we deem the most interesting next steps to be taken by future theoretical work in Section 5. Before that, however, we review recent empirical work that underlines the relevance of the factors listed above and adds additional complexity by highlighting further biological conditions which so far have not been in the center of theoretical attention.

4.1. *Space and territory*

Most species in which agonistic intergroup encounters occur are territorial. Although many of the models reviewed in the previous sections identify territory as the resource most likely to be contested, it has rarely been taken into account explicitly that (i) territoriality imposes a spatial structure on populations that differentiates neighboring groups from groups living farther apart, (ii) different types of territory may differ in their defensibility, (iii) some parts of a given territory may be much more valuable to inhabitants than others, and (iv) experience with a habitat may induce a 'home advantage' for the residents (but see Mesterton-Gibbons and Sherratt, 2016 for a respective dyadic model).

Recent empirical works clearly show, however, that all of these factors play important roles in explaining participation levels in, and occurrence levels of, agonistic intergroup encounters. Roth and Cords (2016), e.g., provide evidence from wild blue monkeys (*Cercopithecus mitis*), showing that residence duration and the spatial proximity of a contested site to the home range center of a group significantly increase this group's chances of successfully defending the site. Markham et al. (2012) also report positive effects of residence duration on contest success in wild baboons (*Papio cynocephalus*). Crofoot and Gilby (2012) present complementary evidence from wild capuchin monkeys (*Cebus capucinus*), for which they find that participation rates in resource defense depend on the location of the contested site within the home range, with participation being 91% more likely at the home range center.

Observations of differential reactions to the type of antagonist, neighbors vs. strangers, are provided by Müller and Manser (2007) for banded mongooses (*Mungos mungo*) and by Bruintjes et al. (2016) for cooperatively breeding cichlid fish (*Neolamprologus pulcher*), both observing stronger reactions to intrusions by neighbors. Furthermore, a systematic comparison of the territoriality regimes of chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and humans (*Homo sapiens*) by Jaeggi et al. (2016) highlights the importance of resource defensibility in explaining the remarkable differences in the occurrence levels of intergroup conflicts between these species. Noteworthy negative findings, finally, are reported by Cassidy et al. (2015), who find no effect of location on conflict outcome in wolves (*Canis lupus*).

4.2. *Between-group differences*

In addition to identifying spatial parameters as important predictors of contest outcomes in many species, most of the works referenced in Section 4.1 also find significant relations of different measures of a group's 'resource holding potential' (RHP) – i.e. combinations of group size, sex ratios and individual level proxies for physical strength – with successful resource defense (Cassidy et al., 2015; Jaeggi et al., 2016; Markham et al., 2012; Roth and Cords, 2016). And although Cassidy et al. (2015) find conflict locations to be unrelated to conflict outcomes, they also report that a relative numerical advantage does predict intergroup conflict success in wolves.

Further instructive evidence comes from a series of papers on fight tactics in various species of ants (*Formicidae*), begun by Franks and Partridge (1993). These papers test whether differences in RHP affect conflict outcomes as would be predicted by Lanchester-type models (see Section 2.2). Although this literature is divided with respect to whether contest success in the studied species depends linearly or non-linearly on numerical differences in party strengths, and if so under which ecological conditions, all of these papers provide evidence that differences in group sizes and individual fighting capabilities have a significant bearing on contest outcomes (see, e.g., Batchelor and Briffa, 2010, 2011; Plowes and Adams, 2005; Tanner, 2006; also see Table S1).

It should also be noted that the empirical literature on the effects of differences in RHP is not limited to the study of conflict outcomes. Using prudent experimental designs, several studies on this question were also able to establish that at least some animals seem to be able to compare their group's RHP to that of an opposing group, and to condition their efforts on this assessment. Wilson et al. (2001), e.g., found that chimpanzees only approach simulated intruders when their numerical advantage is greater than a certain threshold. McComb et al. (1994) found similar reactions in female lions (*Panthera leo*). van Belle and Scarry (2015), furthermore, recently established that black howler monkeys (*Alouatta pigra*) and tufted capuchins (*Sapajus nigritus*) also condition their responses on assessments of relative RHP.

Intriguingly, several studies using comparable methodologies were also able to show that superior RHP comes at the price of a lower individual willingness to participate in conflicts. Crofoot and Gilby (2012), e.g., found that numerically superior groups of capuchins suffered from free-riding by more members when the resource at stake was 'unimportant', i.e. located close to the border of a group's home-range. Similar patterns were observed by Batchelor and Briffa (2011) for red wood ants (*Formica rufa*) and by Bonanni et al. (2010) for wild dogs (*Canis lupus familiaris*). In line with theoretical predictions, such empirical work suggests that collective action problems might be weakening larger groups' RHP (see Section 2). In fact, three recent, remarkable meta-studies based on data from more than a hundred primate species provide strong evidence that this seems to be the case (Willems et al., 2013; Willems et al., 2015; Willems and van Schaik, 2015).

Table 3
Synoptic overview of the contents of this review.

	Description
A formal definition of conflict	Conflicts between (pre-)forms of life arise when at least one of them negatively affects the others' Darwinian fitness, e.g. by interfering with its structural integrity, resource supply, growth, dispersal or reproductive interests.
Foundational studies in biology	Clutton-Brock et al. (1979); Enquist and Leimar (1983, 1990); Hammerstein (1981); Maynard Smith (1974); Maynard Smith and Price (1973); Parker (1974); Wrangham (1999)
Methods used to study conflict	Formal game theoretic modeling Agent-based simulations Naturalist observations Field experiments (e.g. using playbacks to simulate hostile intrusions) Meta-analyses (comparing observations within and across species)
Main models used in the literature	Hawk-Dove games Tullock-contest games Tug-of-war games War-of-attrition games Lanchester-type models

4.3. *Within-group heterogeneity*

To do full justice to the empirical literature, it must also be highlighted that empiricists sophisticatedly account for individual heterogeneity in their observations of animal intergroup conflict behavior. Most studies referenced in this section so far keep detailed track of individual-level differences. Cassidy et al. (2015), for example, carefully control for variance in age and sex in the wolf packs they study and find that both moderate the effect of group size in explaining conflict success. Sex and dominance hierarchy are also found to be decisive factors in explaining whether a given primate species is more or less successful in defending territories in the meta-analyses by Willems and colleagues (Willems et al., 2013; Willems et al., 2015; Willems and van Schaik, 2015). One consistent pattern across species they were able to identify is that philopatry of the dominant sex significantly increases the chances of successful territory defense, i.e. in species where the 'stronger' sex tends to stay with its natal group after adolescence, territory defense is more likely to be effective.

Another exemplary analysis is presented by Mares et al. (2012). Studying cooperatively breeding meerkats (*Suricata suricatta*), they find that dominant males, for whom the costs of losing territory are highest, invest the most in group defense. Carefully tracking proxies of individual fitness, Mares et al. are also able show that group defense has two types of costs for these males: direct energetic costs and opportunity costs, as males cannot help feeding pups while defending. Eventually, Mares et al. find that male meerkats seem to be able to condition their defensive efforts on both types of costs and reduce efforts when their groups contain dependent young. A comparably detailed analysis of how individual-level costs and benefits affect participation in territory defense in blue monkeys (*Cercopithecus mitis stuhlmanni*) revealed strikingly similar patterns (Cords, 2007). Complementary, very complex individual reaction patterns to simulated intrusion threat are reported by Heinsohn and Packer (1995) for female lions.

To conclude: The list of empirical observations presented in this section certainly does not exhaust the set of phenomena worth intensified theoretical attention. Additional important empirical work exists, for example, on pre- and post-conflict affiliative and punishment behavior within groups (Arseneau-Robar et al., 2016; Majolo et al., 2016; Radford, 2008, 2011; Radford et al., 2016) and on within- and between-group genetic differentiation in species with high levels of intergroup conflict (Biernaskie and Foster, 2016; Langergraber et al., 2011). Clearly there is quite a lot of data available and much work waiting for theorists who would like to offer models of animal intergroup conflicts tailored more closely to biological reality.

5. Discussion and outlook

In this paper, we outlined the existing theoretical literature on approaches to modeling animal intergroup conflict behavior in theoretical biology (Section 2), highlighted the intricacies emerging in the process of adding due biological realism to such models (Section 3), and pointed out recent empirical findings that can inspire future theorizing (Section 4); see Table 3 for a synopsis.

In summary, we have seen that a plethora of models of animal intergroup conflict behavior exists using various analytical approaches and differing considerably in their core assumptions. Still, a number of rather general insights can be derived from the existing theoretical literature. One such insight is that the results of models of intergroup conflicts in animals sensitively depend on assumptions about the demographics of the meta-population. A frequently obtained result, e.g., is that conflict occurrence is dampened by higher levels of migration between subgroups. The same holds for increased genetic relatedness between subgroups in models that track this characteristic. Conversely, in extreme scenarios with low migration and a strong impact of between-group conflict on individual fitness, intergroup conflicts are predicted to be more likely to occur and to be more intense. Another general insight is that collective action problems often lead to reduced individual participation in conflicts, both in theory and in the field (see Section 4.2). The picture is more complex, however, for the

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effects of group size. While the benefits of free-riding on collective efforts usually increase with group size, larger groups can still do better in intergroup conflicts, e.g. in finite-*N* models (see Section 3.2) or when group size matters for conflict success (see Section 2.2). Similarly complex patterns emerge for within-group heterogeneity. While homogeneity can lead to higher overall conflict efforts exerted by groups when all individuals have the same stake in the conflict's outcome, stark heterogeneity can have the same effect when those individuals who obtain the highest shares can also exert the highest efforts. In extreme cases, these high-ranking dominant individuals can even over-compensate for the reduced efforts by their subordinate group members (see Section 2.3).

Concluding, the remainder of this section sketches our view on where we would like to see the branch of theoretical biology reviewed here develop next, and which obstacles will need to be overcome in this process.

5.1. Key questions for future research

Perhaps most importantly, we see a need for a major theoretical effort to integrate the existent, but scattered, theoretical insights of the logic of animal intergroup conflict into a unified game theoretical framework. As the previous sections have shown, it is possible to devise consistent notation, from which large parts of the existing models can be parsimoniously reconstructed. Since there are certainly more elegant ways of achieving this than the one we have used here, we are positive that a generic mathematical framework of the logic of animal (intergroup) conflict is not too ambitious a goal. Instructive recent classification work on contest models in economics can also help facilitate this endeavor (Chowdhury and Sheremeta, 2011; Sheremeta, 2015).

Second, as Section 3 has illustrated, existent models differ starkly in their biological background assumptions about population size, demographics, strategy revision protocols, etc. While some of these differences might eventually resolve to mere mathematical subtleties without much empirical bearing (Lehmann et al., 2007), others definitely represent important modeling choices that qualify models' applicability and testability, e.g. the frequent assumption of infinite meta-population size. Therefore, intensified game theoretical research is needed in order to determine more clearly which assumptions are crucial with respect to a model's biological applicability and which are not as decisive. While this research is pending, however, comparative modeling work, as e.g. presented by Lehmann (2011) and Kaiping et al. (2016), will remain indispensable and should, in our view, receive intensified attention.

Third and finally, a closer integration of the existent work on dyadic conflicts with the literature on intergroup conflicts seems like a fruitful prospect. As we have seen in Section 2, the formal overlap between these types of models is large. Thus, it will be a very interesting endeavor to generalize established dyadic models to the intergroup level. In particular, the existing models on alliance formation (Gavrilets et al., 2008; Getty, 1987; Mesterton-Gibbons et al., 2011), eavesdropping (Johnstone, 2001; Mesterton-Gibbons and Sherratt, 2007) and post-conflict victory displays (Bower, 2005; Mesterton-Gibbons and Sherratt, 2006) appear as promising starting points for such efforts to us.

5.2. Challenges for future research

Apart from the obvious problems that (i) increasingly realistic models usually become too complicated to analyze and (ii) the application of more detailed models to explain real-world phenomena requires much more intense data-gathering efforts to be able to empirically calibrate all relevant parameters, we mainly see two obstacles to a quick development of the study of intergroup conflict behavior.

First, the complexity of the subject matter may prompt theorists to resort to the use of simplifying assumptions that drastically reduce the biological realism and applicability of their models. While sufficient simplicity is a natural requirement of formal work, it increases the risk of obtaining theoretical results that are not applicable by empiricists, resulting in models that remain untested.

Second, we see a risk that the obvious synergies attainable in collaborative work by theoretical biologists, economists and colleagues from other disciplines working on formally very similar models of intergroup conflict may remain unexploited. This would be a pity. However, we are positive that the papers collected in this issue will help to significantly reduce this risk and add to encouraging an interdisciplinary exchange of ideas and modeling approaches that facilitates the development of a sufficiently general and empirically grounded theory of intergroup conflict behavior.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jebo.2017.05.004.

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