

Animal network phenomena: insights from triadic games

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Games of animal conflict in networks rely heavily on computer simulation because analysis is difficult, the degree of difficulty increasing sharply with the size of the network. For this reason, virtually the entire analytical literature on evolutionary game theory has assumed either dyadic interaction or a high degree of symmetry, or both. Yet we cannot rely exclusively on computer simulation in the study of any complex system. So the study of triadic interactions has an important role to play, because triads are both the simplest groups in which asymmetric network phenomena can be studied and the groups beyond dyads in which analysis of population games is most likely to be tractable, especially when allowing for intrinsic variation. Here we demonstrate how such analyses can illuminate a variety of behavioral phenomena within networks, including coalition formation, eavesdropping (the strategic observation of contests between neighbors) and victory displays (which are performed by the winners of contests but not by the losers). In particular, we show that eavesdropping acts to lower aggression thresholds compared to games without it, and that victory displays to bystanders will be most intense when there is little difference in payoff between dominating an opponent and not subordinating.

1 Triadic games

The essential ingredients for mathematical analysis of a continuous population game are a well defined reward function f , such that $f(u, v)$ yields the reward to a focal u -strategist in a population of v -strategists, and the concept of an evolutionary stable strategy or ESS (4). Strategy v is a (strong) ESS if it is uniquely the best reply to itself, i.e., if $f(v, v) > f(u, v)$ for all $u \neq v$.

Two kinds of continuous triadic game of conflict have proven especially amenable to analysis. The first kind of game, which we call Type I, is one in which strategies are intensities, variance of fighting strength is zero, and the set of all possible outcomes from the triadic interaction has a discrete probability distribution for every conceivable strategy combination (u, v) . Let there be K such outcomes in all, let $w_i(u, v)$ be the probability associated with outcome i and let $P_i(u)$ be the corresponding payoff to the focal individual. Then

$$f(u, v) = \sum_{i=1}^K w_i(u, v) P_i(u, v) \quad \text{with} \quad \sum_{i=1}^K w_i(u, v) = 1. \quad (1)$$

The second kind of game, which we call Type II, is one in which strategies are thresholds, variance of strength is non-zero and strength is continuously distributed with probability density function g on $[0, 1]$; nevertheless, for all (u, v) the sample space $[0, 1]^3$ of the triad's three strengths—assumed independent—can be decomposed into a finite number K of mutually exclusive events. Let $\Omega_i(u, v)$ denote the i -th such event, and let $P_i(X, Y, Z)$ denote the corresponding payoff to the focal individual when its strength is X and the other two strengths in the triad are Y and Z . Then

$$f(u, v) = \sum_{i=1}^K \iiint_{\substack{(x, y, z) \\ \in \Omega_i(u, v)}} P_i(x, y, z) g(x) g(y) g(z) dx dy dz. \quad (2)$$

We provide examples of each kind of game.

2 Victory displays

Victory displays, ranging from sporting laps of honor to military parades, are well known in human societies and have been reported in various other species (1), the best known example being the celebrated “triumph ceremony” of the greylag goose (3). Two models of such victory displays exemplify the Type I game.

Bower (1) defined a victory display to be a display performed by the winner of a contest but not the loser. He proposed two explanations for their function. The “advertising” rationale is that victory displays are attempts to communicate victory to other members of a social group that do not pay attention to contests or cannot otherwise identify the winner. The “browbeating” rationale is that

victory displays are attempts to decrease the probability that the loser of a contest will initiate a future contest with the same individual. Our models—distinguished by A for advertising and B for browbeating—explore the logic of these rationales.

Both models assume that the members of a triad participate in three pairwise contests, and that more intense victory displays are more costly to an individual but also more effective in terms of either being seen by conspecifics (Model A) or deterring further attack (Model B): at intensity s , the cost of signalling is $c(s)$, and the probability of the desired effect is $p(s)$. In either model, dominating another individual increases fitness by α , and a contest in which neither individual dominates the other increases the fitness of each by $b\alpha$, where $b \leq 1$.

In Model A, we assume that a bystander that has seen an individual win will subsequently defer to it with fixed probability λ_i , where $i = 0$, $i = 1$ or $i = 2$ according to whether the observer is an untested individual, a prior loser or a prior winner, respectively, with $0 \leq \lambda_2 \leq \lambda_0 \leq \lambda_1 \leq 1$. Deferring eliminates the cost of a fight, which we denote by c_0 . We also allow for a prior loser to defer to an observed loser with probability λ_3 , and we allow for a potential “loser effect” (8): an (indirectly) observed loser subsequently loses against the observer with probability $\frac{1+l}{2}$ where $0 \leq l \leq 1$.

The reward function is most readily obtained by first recording the payoffs and probabilities associated with each outcome in a table having K rows; then (1) determines f . Because $K = 36$ for Model A, however, only excerpts are shown as Table 1: the full table appears in (7). As presented, the table assumes that displays are obligate. One could argue, however, that—at least among animals with sufficient cognitive ability—victory displays should be facultative: in a triadic interaction, there is no need to advertise after an individual’s final contest, because there is no other individual that can be influenced by the display. Our model is readily adapted to deal with this possibility, as described in (7).

For the sake of definiteness, we analyze the game with

$$c(s) = \gamma\theta\alpha s, \quad p(s) = \epsilon + (1 - \epsilon)(1 - e^{-\theta s}) \quad (3)$$

where $\theta (> 0)$ has the dimensions of INTENSITY^{-1} , so that $\gamma (> 0)$ is a dimensionless measure of the marginal cost of displaying, and $0 \leq \epsilon \leq 1$. The analysis shows that for any values of the positive parameters c_0 , γ , l , b , λ_0 , λ_1 , λ_2 and λ_3 (the last six of which cannot exceed 1), there is a unique ESS at which animals display when ϵ —the baseline probability of observing victors in the absence of a display—lies below a critical value, but otherwise do not display. This critical value is zero if display cost γ is too large but otherwise positive; it decreases with respect to γ or l , increases with respect to any of the other six parameters and is higher for facultative than for obligate signallers (except that it is independent of λ_3 for facultative signallers). For subcritical values of baseline probability of observation ϵ , the intensity of signalling at the ESS decreases with respect to γ or l , increases with respect to any of the other six parameters and is higher for facultative than for obligate signallers (with the same exception as before). Moreover, it largely does not matter whether the effect of signalling is

interpreted as increasing the probability of being seen or of being deferred to.

Table 1: Model A payoff to a focal individual F whose first and second opponents are O1 and O2, respectively, conditional on participation in the last two of the three contests. Parentheses indicate a contest in which the focal individual is not involved. A bold letter indicates that the individual's opponent deferred. Note that O1 and O2 do not label specific individuals: O1 is whichever individual happens to be the focal individual's first opponent for a given order of interaction, the other individual is O2.

CASE	WINNERS			PROBABILITY	PAYOFF
i	1st	2nd	3rd	$w_i(u, v)$	$P_i(u)$
1	F	F		$\frac{1}{6}\lambda_0 p(u)$	$\{2 - 2c(u) - c_0\}\alpha$
2	F	F		$\frac{1}{12}\{1 - \lambda_0 p(u)\}$	$\{2 - 2c(u) - 2c_0\}\alpha$
5	O1	O2		$\frac{1}{12}\{1 + lp(v)\}$	$-2c_0\alpha$
8	F	(O2)	F	$\frac{1}{12}\{1 + lp(u)\}\{1 - \lambda_2 p(v)\}\lambda_2 p(u)$	$\{2 - 2c(u) - c_0\}\alpha$
9	F	(O2)	F/O2	$\frac{1}{12}\{1 + lp(u)\}\lambda_2^2 p(v)p(u)$	$\{1 + b - c(u) - c_0\}\alpha$
10	F	(O2)	F	$\frac{1}{24}\{1 + lp(u)\}\{1 - \lambda_2 p(u)\}\{1 - \lambda_2 p(v)\}$	$\{2 - 2c(u) - 2c_0\}\alpha$
29	(O1)	F	O2	$\frac{1}{24}\{1 - \lambda_0 p(v)\}\{1 - \lambda_1 p(u)\}\{1 - lp(v)\}$	$\{1 - c(u) - 2c_0\}\alpha$
33	(O2)	O1	O2	$\frac{1}{12}\{1 - lp(v)\}\lambda_1 p(v)$	$-c_0\alpha$
36	(O1)	O1	F/O2	$\frac{1}{12}\{1 - \lambda_0 p(v)\}\lambda_3^2$	$\{b - c_0\}\alpha$

In Model B, we assume that contestants subordinate to a current winner with a probability that increases with the intensity of the victory display, and we re-interpret ϵ as the baseline probability of submission (i.e., the probability that a victor elicits permanent submission from a loser in the absence of a display). As before, we construct a table of payoffs and associated probabilities. Because the order of interaction does not matter in this case, there are fewer possible outcomes; specifically, $K = 10$ in (1). We again find that there is a unique ESS with a critical value of ϵ , above which winners do not display, below which intensity decreases with ϵ (7).

In this regard, predictions from the models are similar; however, there is also an important difference. In the case of advertising, the intensity of display at the ESS increases with respect to the parameter b , an inverse measure of the reproductive advantage of dominating an opponent compared to simply not subordinating; by contrast, in the case of browbeating, the intensity of display at the ESS decreases with respect to b , as illustrated by Fig. 1. Therefore, all other things being equal, the intensity of advertising victory displays will be highest when there is little difference between dominating an opponent and not subordinating, a set of conditions likely to generate low reproductive skew (as in monogamous species). By contrast, the intensity of browbeating victory displays will be highest when there are greater rewards to dominating an opponent, a set

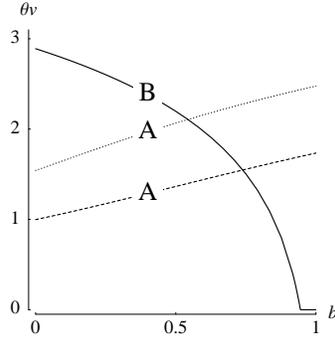


Figure 1: Comparison of advertising and browbeating ESSs. Evolutionarily stable signalling intensity (scaled with respect to $\frac{1}{\theta}$ to make it dimensionless) is plotted as a function of dominance advantage b . Values of the other parameters (all dimensionless) are $c_0 = 0.1$ for the fixed cost of a contest, $l = 0.5$ for the loser effect (i.e., the probability that an observed loser again loses is 0.75), $\gamma = 0.05$ for the marginal cost of displaying, $\lambda_i = 0.9$ for all i for the probability of deference and $\epsilon = 0.1$ for the baseline probability of the desired effect (bystander attention to victor in Model A, submission to current opponent in Model B) in the absence of a display. For obligate signallers, the advertising ESS is shown dashed; for facultative signallers, it is shown dotted.

of conditions that is likely to generate high reproductive skew. These predictions appear to accord quite well with our current understanding of the taxonomic distribution of victory displays (1; 7).

3 Coalition formation

A model of coalition formation exemplifies the Type II game. We merely sketch this model here; full details are in (5).

We assume that each member of a triad knows its own strength but not that of either partner. All three strengths are drawn from the same symmetric Beta distribution on $[0, 1]$ with variance σ^2 . Stronger animals tend to escalate when involved in a fight, weaker animals tend to not to escalate. If an animal considers itself too weak to have a chance of being the alpha (dominant) individual in a dominance hierarchy, then it attempts to form a coalition with everyone else: coalition means a mutual defence pact and an equal share of benefits. Let Λ denote total group fitness. Then it costs $\theta\Lambda$ (≥ 0) to attempt a coalition; the attempt may not be successful, but if all agree to it, then there are no fights.

If there's a dominance hierarchy with three distinct ranks after fighting, then the alpha individual gets $\alpha\Lambda$ (where $\alpha > \frac{1}{2}$), the beta individual gets $(1 - \alpha)\Lambda$ and the gamma individual gets zero. If there's a three-way coalition or if the animals fight one another and end up winning and losing a fight apiece, then each gets $\frac{1}{3}\Lambda$; however, in the second case they also incur a fighting cost. If a coalition of two defeats the third individual, then each member of the pair

Table 2: Payoff to a focal individual F of strength X whose partners are A and B with strengths Y and Z , respectively, with $\Delta = q\{X + Z\} - Y$ and $\zeta(X, Y, Z) = \alpha p(X - Y)p(X - Z) + \frac{1}{3}\{p(X - Y)p(Z - X)p(Y - Z) + p(X - Z)p(Y - X)p(Z - Y)\} + (1 - \alpha)\{p(X - Y)p(Z - X)p(Z - Y) + p(X - Z)p(Y - X)p(Y - Z)\}$.

CASE i	COALITION STRUCTURE	EVENT $\Omega_i(u, v)$	PAYOFF $P_i(X, Y, Z)$
1	$\{F, A, B\}$	$X < u, Y < v, Z < v$	$\{\frac{1}{3} - \theta\}\Lambda$
2	$\{F, B\}, \{A\}$	$X < u, Y > v, Z < v$	$\frac{1}{2}\{\alpha p(\Delta) + 1 - \alpha - 2\theta - c(\Delta)\}\Lambda$
3	$\{F, A\}, \{B\}$	$X < u, Y < v, Z > v$	$P_2(X, Z, Y)$
4	$\{F\}, \{A, B\}$	$X > u, Y < v, Z < v$	$\{\alpha p(X - q\{Y + Z\}) - c(X - q\{Y + Z\})\}\Lambda$
5	$\{F\}, \{A\}, \{B\}$	$X < u, Y > v, Z > v$	$-\theta\Lambda$
6	$\{F\}, \{A\}, \{B\}$	$X > u, Y > v, Z < v$	$\{(2\alpha - 1)p(X - Y) + 1 - \alpha - c(X - Y)\}\Lambda$
7	$\{F\}, \{A\}, \{B\}$	$X > u, Y < v, Z > v$	$\{(2\alpha - 1)p(X - Z) + 1 - \alpha - c(X - Z)\}\Lambda$
8	$\{F\}, \{A\}, \{B\}$	$X > u, Y > v, Z > v$	$\{\zeta(X, Y, Z) - c(X - Y) - c(X - Z)\}\Lambda$

obtains $\frac{1}{2}\Lambda$ while the individual obtains zero; and if the individual defeats the pair, then it obtains $\alpha\Lambda$ while each member of the pair obtains $\frac{1}{2}(1 - \alpha)\Lambda$. We assume that there is at least potentially a synergistic effect, so that the effective strength of a coalition of two whose individual strengths are S_1 and S_2 is not simply $S_1 + S_2$ but rather $q\{S_1 + S_2\}$, where q need not equal 1.

Let $p(\Delta s)$ denote the probability of winning for a coalition (or individual) whose combined strength exceeds that of its opponent by Δs ; p increases sigmoidally with Δs at a rate determined by a parameter r measuring the reliability of strength difference as a predictor of fight outcome. Note that $p(\Delta s) + p(-\Delta s) = 1$ with $p(-2) = 0$, $p(0) = \frac{1}{2}$ and $p(2) = 1$. We assume that fighting costs are equally borne by all members of a coalition. Let $c(\Delta s)\Lambda$ be the cost of a fight between coalitions whose effective strengths differ by Δs . Costs are greater for more closely matched opponents; so, from a maximum c_0 , cost decreases nonlinearly with $|\Delta s|$ at a rate determined by a parameter k measuring sensitivity of cost to strength difference.

Let u be the coalition threshold for Player 1, the potential mutant: if its strength fails to exceed this value, then it attempts to make a mutual defence pact with each of its conspecifics. Let v be the corresponding threshold for Player 2, who represents the population. Let X be the strength of the u -strategist, and let Y and Z be the strengths of the two v strategists. We can now describe the set of mutually exclusive events with associated payoffs as in Table 2, and the reward follows from (2) with $K = 8$.

For this game, the evolutionarily stable strategy set depends on seven parameters, namely, c_0 (maximum fighting cost), q (synergy multiplier), θ (pact cost), α (proportion of additional group fitness to a dominant), r (reliability of strength difference as predictor of fight outcome), k (sensitivity of cost to

strength difference) and σ^2 (variance). It is a complicated dependence, but it enables us to calculate, among other things, the probability that two animals will make a pact against the third in an ESS population. Details appear in (5).

4 Eavesdropping

As noted in §2, animals can eavesdrop on the outcomes of contests between neighbors and modify their behavior towards observed winners and losers. A model of such eavesdropping (6) further exemplifies the Type II game, in this case with $K = 28$.

The model, which extends the classic Hawk-Dove model of animal conflict to allow for both continuous variation in fighting ability and costs that are greater for more closely matched opponents (as in §3), was motivated by earlier work showing that eavesdropping actually increases the frequency of mutually aggressive contests (2). But that conclusion was predicated on zero variance of strength.

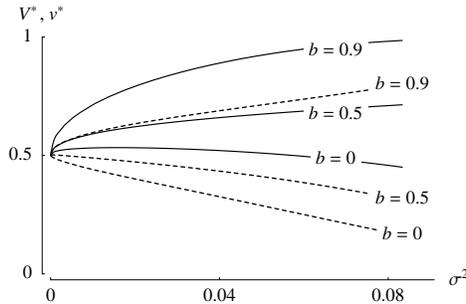


Figure 2: The evolutionarily stable aggression threshold under eavesdropping (V^* , solid curve) as a function of variance σ^2 for various values of the dominance advantage parameter b when strength has a symmetric Beta distribution on $[0, 1]$ and the cost of a fight between animals whose strengths differ by Δs is $1 - |\Delta s|^{0.2}$ for $\Delta s \in [-1, 1]$. In each case, the corresponding basic threshold (v^* , dashed curve) is also shown.

To obtain a tractable model with non-zero variance, we had to make several simplifying assumptions. In particular, we assumed that fights are always won by the stronger animal (the limit of §3 as reliability parameter $r \rightarrow \infty$). Furthermore, we first determined a basic aggression threshold for animals that do not eavesdrop, and then considered eavesdropping only among animals whose strengths at least equal that basic threshold. Thus the question becomes whether eavesdropping raises the threshold. We found that it always does, suggesting that eavesdropping reduces rather than increases aggressive behavior in Hawk-Dove games. Typical results are shown in Fig. 2, where the parameter b has the same meaning as in §2. Details appear in (6).

5 Conclusion

We have shown how to obtain insights on animal network phenomena by studying them in their simplest possible setting, namely, a triad. Our analysis of victory displays (Type I, strategies as intensities) has confirmed that such behavior can occur either as an advertisement to bystanders or to browbeat a current opponent. Our analyses of coalition formation and eavesdropping (Type II, strategies as thresholds) have helped elucidate the fundamental conditions under which coalitions will form, and indicate for the first time that eavesdropping acts to reduce the frequency of escalated fighting in Hawk-Dove models. We hope that our analyses of these triadic interactions serve as important benchmarks for understanding analogous phenomena in larger networks.

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