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Multiple Asymmetry and Concord Resolutions of a Conflict

ILAN ESHEL*† AND EMILIA SANSONE‡

**Department of Statistics, School of Mathematics, Tel Aviv University, Israel and ‡Department of Mathematics and its Applications, University of Naples, Naples, Italy*

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A model for a population-game with multiple asymmetry is studied, in which the participants are assumed to be different from one another both in size and in status as owners or non-owners of a territory. Only owners can reproduce, hence natural selection is assumed to operate in favor of the increase of ownership-time. Conditions for the evolutionary stability of the Bourgeois Principle of owner-priority, despite difference in body size, are characterized. It is shown that ownership-priority tends to be at least partially replaced by strength-priority as the availability of habitats, the expected longevity of potential intruders and the harm inflicted on the loser of an aggressive confrontation decrease, and as the expected longevity of the owner increases. It is further established that the combined effect of all these parameters can be characterized by a single parameter, referred to as the concord coefficient of the population. Finally, when this parameter reaches a certain critical level, only strength-priority can prevail. If the concord coefficient decreases below this critical level, no priority-rule can remain stable in the population, in which case aggressive confrontations cannot be avoided, at least in certain situations. In this case, it is shown that aggression emerges first among low-rank individuals.

1. Introduction

As it was first demonstrated in the seminal work of Maynard Smith & Parker (1976), and later on, in a more general context, by Selten (1980), any recognizable asymmetry between participants of a population-game may drastically affect their evolutionarily stable strategies. It was further demonstrated by Maynard Smith and Parker that this may be true even for a *non-essential* asymmetry which, given the strategies of the participants, bears no direct effect on the outcome of the game. Such a phenomenon becomes apparent in conflicts of the hawk–dove type, where encountered individuals each aim to a different outcome, but in which an aggressive confrontation between them is in the worst interest of both. Any equilibrium, notwithstanding an ESS of the symmetric version of such a population-game, is easily shown to be a mixed, *discord strategy*, namely a strategy that, at least in some positive probability, leads to an aggressive confrontation. On the other hand, it has been proved by Selten (1980) that no mixed ESS is possible for any asymmetric population-game. For the asymmetric version of the hawk–dove population-game we know, moreover, that if the risk of confrontation is sufficiently high, the only evolutionarily stable strategies are *concord strategies*, namely such that lead to no aggressive confrontation. Thus, any sort of a recognizable asymmetry between the participants may serve, in such a case,

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†Author to whom correspondence should be addressed.

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to establish an evolutionarily stable priority rule, preventing aggressive confrontation, otherwise inevitable.

Natural conflicts, however, are quite generally characterized by more than one parameter of asymmetry. A natural question to be asked then is which parameter (or parameters) of asymmetry is likely to be accepted by the participants and under what conditions the acceptance of such a parameter should serve as a basis for a concord stable strategy in the population (e.g. see Hammerstein, 1981). In the present work, we shall concentrate on the case of a two-dimensional asymmetry. Following Maynard Smith and Parker, we assume that individuals in the population can either be owners of a territory or potential intruders; like Hammerstein, though, we further assume that they may be of different body size. Ownership may be easier to immediately recognize, yet body size is likely to be more directly correlated with strength. We assume a life-history model in which individuals that lose a territory, yet staying alive, still have a chance to find another one in the future. Concentrating on a situation in which ownership of a territory is a necessary condition for reproduction, it is assumed that natural selection is operating on the expected length of time one finds himself as an owner of a territory (e.g. see Eshel & Sansone, 1995).

We first characterize the new conditions under which the Bourgeois Principle of owner-priority, suggested by Maynard Smith and Parker, remains evolutionarily stable in face of differences in body size. We see, however, that in such a case, even when the Bourgeois Principle is an ESS, so is a set of more complicated "natural" rules, combining ownership and body size. We see under which conditions such rules inevitably replace the Bourgeois Principle and under which conditions body-size priority alone is the basis for the only concord stable strategy in the population. Finally, we see under what conditions no such concord strategy can possibly exist. Differently from what is known to be the case in a situation of a one-dimensional asymmetry, we shall see that in the case of multiple asymmetry, the failure of all concord stable strategies does not necessarily entail their replacement by a totally aggressive one. More likely, the resulting discord stable strategies are characterized by a specific subset of situations under which aggressive confrontation is inevitable, while some concord priority-rule is still respected in the other. Only under quite extreme conditions, total aggression is expected to take place.

It is shown that ownership-priority tends to be replaced by strength-priority and later on by discord aggression as the availability of habitats, the expected longevity of the potential intruder and the harm inflicted on the loser of an aggressive confrontation decrease, and as the expected longevity of the owner increases. Not surprisingly, it is shown that the first to challenge the Bourgeois Principle, thus giving room to multi-factor priority rules, are potential intruders of large body size, when encountering owners of small body size. Body-size priority, on the other hand, is first challenged by individuals of small body size, either owner or intruders, when they encounter opponents of slightly larger size. This last finding is suggested as an explanation for the observed phenomenon of a different behavior of high- and low-rank individuals towards their subordinates (e.g. Lorenz, 1963).

2. On the Maintenance of the Bourgeois Principle in Face of Life-history Expectation of Ownership-time

The first and most widely discussed concord resolution of an asymmetric conflict in a population was the Bourgeois Principle, suggested by Maynard Smith & Parker (1976) for a conflict between an owner of a territory and a potential intruder. It was assumed that the only information available to the contenders concerned the question of which of them is the owner and which is the intruder. It was further assumed that each of the contenders might choose a strategy of either a hawk or a dove. Doves, when encountering each other, tend to share the territory, and they peacefully yield to any encountered hawk, either owner or intruder. An encounter between two hawks, however, inevitably ends up with an aggressive confrontation in which the probability that the intruder wins is $0 < p \leqslant 1/2$, $q = 1 - p$ being the probability that the owner wins. In either case, the winner takes over the territory while the loser has a probability $0 < \theta \leqslant 1$ to lose his life in the conflict, θ being referred to as *the risk coefficient*. Under the assumption that holding a territory adds a value $v > 0$ to the reproductive value of the owner, Maynard Smith and Parker have characterized the owner–intruder conflict by the game matrix

$$\begin{array}{lcccc} & \multicolumn{2}{c}{\text{Dove}} & \multicolumn{2}{c}{\text{Hawk}} \\ \hline \text{Dove} & v/2 & v/2 & v & 0 \\ \text{Hawk} & 0 & v & qv - p\theta & pv - q\theta \end{array} \tag{1}$$

One can easily characterize the ESS's of this population-game, as corresponding to the following two cases:

Case I: $v \geqslant \theta q/p$

This case is characterized by a relatively high value of a territory and low risk coefficient, "*Always Play Hawk*" is then the only ESS of the conflict. Aggressive confrontation is inevitable and we then speak of a *discord* ESS.

Case II: $v < \theta q/p$

This case is characterized by a relatively low reproductive value of a territory and high risk coefficient. In such a situation:

(a) The "*Bourgeois Principle*" of "Playing Hawk If Owner And Dove If Intruder" is always an ESS of the conflict.

(b) In some cases (i.e. if $v < \theta p/q$), the "*Paradoxical*" strategy of "Playing Hawk If Intruder And Dove If Owner" is also an ESS.

(c) There is no other ESS of the conflict.

In such a case, no aggressive confrontation is possible and we speak of a *concord* ESS.

As noticed by Maynard Smith and Parker, these results remain valid even in the limit case $p = 1/2$ in which owner and intruder have equal chance to win. This is quite interesting because in such a case, the payoff-matrix (1) corresponds to a symmetric game, readily recognized as that of the hawk–dove one. Yet, we know that the only ESS of the latter is the mixed (discord) strategy of playing hawk in probability v/θ and dove in probability $1 - v/\theta$.

The applicability of the Bourgeois Principle to natural owner–intruder conflicts was questioned, however, by Grafen (1987), on the basis of the lack of a reproductive alternative thereby left to the potential intruder. Consistently following the Bourgeois Principle, a potential intruder may remain alive at any given encounter, but with little chance to ever get hold of a territory in the future. Thus, if holding a territory is necessary for reproduction, he is likely to end up leaving no offspring to follow his strategy.

Following Grafen, it was suggested (Eshel & Sansone, 1995) that the expected reproductive success of an individual should be measured by the length of time this individual, either an owner or a potential intruder, is expected to hold a territory in the future. A strategy Γ of a player, in such a case, should be a list of rules determining his behavior at any encounter to come, given his position (i.e. owner or intruder) at the moment of the encounter. Following Maynard Smith and Parker, it was assumed that ownership is the only information available to the contenders, an assumption to be later relaxed here. Following Grafen, it was assumed, though, that in choosing a strategy, each player seeks to maximize his *Expected Ownership Time*, say his EOT. It was further assumed that at any infinitesimal time interval $\mathrm{d}t$, regardless of past events, the following hold:.

(a) An owner of a territory has a probability $\mu\,\mathrm{d}t$ to die out of some natural cause.

(b) He has a probability $\beta\,\mathrm{d}t$ to be encountered by a potential intruder.

(c) A potential intruder has a probability $\lambda\,\mathrm{d}t$ to die out of natural cause.

(d) He has a probability $\alpha\,\mathrm{d}t$ to find a territory, either occupied or empty.

(e) In a steady state, a proportion c of the territories are empty, $c > 0$, if only for the natural death of owners. (Thus, if an empty habitat becomes available only with the natural death of its owner, then $c = \mu/(\beta + \mu)$.)

Given these postulates, any population strategy Γ determines the EOT's T_1 and T_2 of a potential intruder and of an owner, respectively. It is assumed that, given the population strategy, each player attempts to maximize his own EOT. Let us first look for *Agent Equilibria* (Selten, 1975) and, moreover, for *Agent Stable Strategies*, say ASS (Eshel & Shaked, 2001). In agent equilibrium we refer to a strategy Γ which, when fixed in the population, determines the best behavior of any single individual at any given encounter. In ASS we mean an agent equilibrium strategy that, in addition, is a strictly best solution against itself, except, maybe, in events of probability zero. Note that in the general case, the requirement of ASS guarantees only stability against local changes of a strategy, hence it is only a necessary condition for an ESS, the latter also guaranteeing stability against global change. In Appendix A it is shown, however, that in the present model, agent stability implies evolutionary stability.

Suppose that, given a population-strategy Γ, the probability that a potential intruder would ever get hold of a territory before dying is Q_Γ. The expected ownership time T_1 of a potential intruder is, then, equal to the probability Q_Γ, multiplied by his conditional EOT, T_2, once he becomes an owner. Thus,

$$T_1 = Q_\Gamma T_2. \tag{2}$$

Suppose that, given the population strategy Γ, a player knows that his opponent is not expected to yield and that his probability to win a contest of power against such an opponent is p. Yielding, he can always remain with an EOT of T_1. Challenging his opponent, on the other hand, he would have a probability p to become owner with a conditional EOT of T_2, and a probability $(1-p)(1-\theta)$ to lose but remain alive with a conditional EOT of T_1. All in all, he would then get an EOT of $pT_2 + (1-p)(1-\theta)T_1$. Yielding would therefore be the best strategy for the player in question if and only if $T_1 \geqslant pT_2 + (1-p)(1-\theta)T_1$. Inserting eqn (2), this condition becomes

$$Q_\Gamma \geqslant \frac{p}{p+\theta(1-p)}. \tag{3}$$

Assume now that the Bourgeois Principle is accepted in the population. At any infinitesimal time interval dt, a potential intruder has a probability $\alpha c\,\mathrm{d}t$ to find an empty territory, which is his only chance to become an owner and a probability $\lambda\,\mathrm{d}t$ to die. Hence, his probability to ever become an owner before dying is

$$Q_\Gamma = \frac{\alpha c}{\alpha c + \lambda}. \tag{4}$$

From eqns (3) and (4), it thus follows that potential intruders should be better off respecting the Bourgeois Principle, once accepted in the entire population, if and only if, $\alpha c/(\alpha c + \lambda) \geqslant p/[p + \theta(1-p)]$. This readily yields the condition $p \leqslant \alpha\theta c/(\alpha\theta c + \lambda)$ necessary for the agent stability and hence for the evolutionary stability of the Bourgeois Principle, a sufficient condition being

$$p < \frac{\alpha\theta c}{\alpha\theta c + \lambda}. \tag{5}$$

In Appendix A, it is shown that eqn (5) is, moreover, a sufficient condition for the evolutionary stability of the Bourgeois Principle, hence the Bourgeois Principle is an ESS if eqn (5) holds and only if it holds at least as a weak inequality.

We now define a single parameter $R = R(\alpha, \theta, c, \lambda)$, referred to as the *Concord Coefficient*:

$$R = \frac{\alpha\theta c - \lambda}{\alpha\theta c + \lambda}. \tag{6}$$

Employing this notation, eqn (5) becomes

$$p - q \leqslant R. \tag{7}$$

As it follows from eqn (6), the concord coefficient R has values between -1 and 1. It is an increasing function of the availability αc of new habitats, and of the risk θ of aggressive confrontation. It is a decreasing function of the intensity λ of natural death of the potential intruders. In the special case $c = \mu/(\beta + \mu)$, where habitats become empty only with the natural death of their owner, one can easily verify that R is an increasing function of α, θ and μ, and a decreasing function of λ and of the intensity β. From eqn (7) it follows that the larger the value of R, the larger is the range of parameters for which a stable concord resolution of the conflict exists. We shall see that this is true for a more general set of situations.

3. On the Maintenance of the Bourgeois Principle in Face of Differences in Body Size

Some essential asymmetry in natural conflicts between owner and intruder has been attributed by Maynard Smith and Parker to the fact that by succeeding in holding a territory, an owner has already proved to be stronger, on the average, than the potential intruder. A natural question to be asked, though, concerns the possible stability of the Bourgeois Principle when physical strength can be recognized by a marker, more direct than ownership. Assume, for example, that individuals in the adult population are different from one another by body size. Assume that an individual of size x has a probability $p(x, y)$ to win a contest with an individual of size y, $p(x, y)$ being a continuous increasing function of x and a continuous decreasing function of y. Indeed, $p(x, y) + p(y, x) = 1$. Let $F(x)$ and $G(x)$ be the distributions of body size among individuals without and with a territory, respectively, then

$$p = \iint p(x, y)\,\mathrm{d}F(x)\,\mathrm{d}G(y). \qquad (8)$$

But in this case it is most natural to suppose that each individual in the population is fully aware of both his body size and that of his opponent. If, despite differences in body size, the Bourgeois Principle is accepted as a rule in the population, then the probability Q_r of a conformist potential intruder to ever get hold of a territory before dying remains independent of his body size. His chance $p(x, y)$ to win a contest, if challenging the owner's right, depends, however, on both his body size x and the body size y of his opponent. Thus, by repeating the argument given in the previous section, we know that yielding is indeed the best strategy for the intruder if and only if

$$p(x, y) - p(y, x) \leqslant R, \qquad (9)$$

where R is given by eqn (6).

The Bourgeois Principle would thus be an ESS if eqn (9) holds as a strict inequality for all possible body sizes x and y in the population, and only if it holds, at least as a weak inequality. Let x_1 and x_2 be the body size of the smallest and the largest individual in the population, respectively. The condition for evolutionary stability of the Bourgeois Principle in face of body-size differences then becomes

$$p(x_2, x_1) - p(x_1, x_2) \leqslant R. \qquad (10)$$

This condition can be maintained if body size (or any other marker) is a sufficiently poor predictor of strength, if the harm θ inflicted on the loser is sufficiently high, and if the probability $\lambda/(\alpha c + \lambda)$ of dying before ever encountering an empty territory is sufficiently low. A natural question to be addressed is what happens when these conditions are not met. In the next section, we see that, unlike in the one-dimensional situation described by Maynard Smith and Parker, the failure of the stability condition for the Bourgeois Principle does not necessarily entail an inevitable resorting to an aggressive settlement of the owner–intruder conflict. Instead, we see that as long as $R \geqslant 0$, alternative concord priority rules emerge, which incorporate body size or other direct markers of strength. In Section 5, we deal with the situation in which the concord coefficient R is negative.

4. What Happens when the Bourgeois Principle Fails? On the Emergence of Alternative Priority Rules

Suppose condition (10) for the agent stability of the Bourgeois Principle does not hold. We now see that a set of natural concord rules can remain stable, in which the Bourgeois Principle is still accepted by contenders of a not too big difference in body size.

Definition. Denote by x the body size of the intruder and by y that of the owner. For any real value $0 \leqslant k \leqslant 1$ define a strategy Γ_k, determining the following behavior on the part of both owner and potential intruder:

(a) Whenever $p(x, y) - p(y, x) \leqslant k$, accept the Bourgeois Principle.

(b) Whenever $p(x, y) - p(y, x) > k$, accept the priority of the larger body size.

For $k \geqslant p(x_2, x_1) - p(x_1, x_2)$, Γ_k is indeed the Bourgeois Principle. For $k = 0$ it determines an alternative one-dimensional rule of priority, based exclusively on body size, say *the Strength-priority rule.* For $0 < k < p(x_2, x_1) - p(x_1, x_2)$, Γ_k determines a combination of the two rules, in which the relative weight of the Bourgeois Principle increases with the parameter k.

We shall refer here to the strategies Γ_k, defined above, as *Natural Priority Rules*, and in dealing with concord population strategies we thereby restrict ourselves to such priority rules. Note, however, that other concord population strategies can be defined and, under sometime plausible conditions, prove stable, *the Paradoxical ESS* mentioned above being only one of them. More generally, for any two non-intersecting measurable sets A, B in $[0, 1]$ define the following rule: "Owner-priority if the difference in body size falls within A, Intruder-priority if the difference in body size falls within B, and Strength-priority elsewhere".

Assume now that the strategy Γ_k is already accepted as a rule in the population. Γ_k is an ESS if and only if, for any contender, either owner or intruder that according to Γ_k is expected to yield, yielding is indeed the best strategy. (Given this, his opponent would obviously be satisfied with non-yielding, which is his Γ_k-strategy.) Thus, following the definition of Γ_k and ignoring events of probability zero, Γ_k is an ESS if and only if:

(a) Whenever $p(x, y) - p(y, x) < k$, yielding, which in this case is the Γ_k- strategy for the potential intruder, is also his best.

(b) Whenever $p(x, y) - p(y, x) > k$, yielding, which in this case is the Γ_k- strategy for the owner, is at the same time the owner's best strategy.

Let us first consider a potential intruder of body size x. As we recall, he has a chance of $\alpha\,\mathrm{d}t$ to find a territory, either empty or occupied, within an infinitesimal time interval $\mathrm{d}t$. Define by $c_{x,k}$ the conditioned probability that the found territory would be available for him, given his body size x and the population strategy Γ_k. This would occur either if this territory were empty or else if it is occupied by an owner of body size y for which $p(x, y) - p(y, x) > k$, hence,

$$c_{x,k} = c + (1 - c) \int_{p(x,y) - p(y,x) > k} \mathrm{d}G(y). \quad (11)$$

The probability that the potential intruder in question would find and get hold of a territory within an infinitesimal time interval $\mathrm{d}t$ is, therefore, $\alpha c_{x,k}\,\mathrm{d}t$. Recalling that his chance to die within that time interval is $\lambda\,\mathrm{d}t$, we know that his chance to ever get hold of a territory before dying is

$$Q_k(x) = \frac{\alpha c_{x,k}}{\alpha c_{x,k} + \lambda}. \quad (12)$$

Assume now a contender of body size x (either an owner or a potential intruder) who encounters a determined opponent of body size y. Repeating the arguments given in Section 2 with $Q_r = Q_k(x)$ and $p = p(x, y)$, condition (3) for the advantage of yielding (now for this specific player in this specific situation) becomes

$$Q_k(x) \geqslant \frac{p(x, y)}{p(x, y) + \theta[1 - p(x, y)]}. \quad (13)$$

Inserting eqn (12) into eqn (13) and recalling that $1 - p(x, y) = p(y, x)$, this condition can readily be written as

$$p(x, y) - p(y, x) \leqslant \frac{\theta\alpha c_{x,k} - \lambda}{\theta\alpha c_{x,k} + \lambda}. \quad (14)$$

The requirement (i) for the stability of Γ_k against intruder's over-aggression is, therefore, satisfied if and only if, eqn (14) holds for all x and y for which $p(x, y) - p(y, x) \leqslant k$. For a fixed value of x this means that if $p(x, y) - p(y, x) \leqslant k$, then $p(x, y) - p(y, x) \leqslant (\theta\alpha c_{x,k} - \lambda)/(\theta\alpha c_{x,k} + \lambda)$. A necessary and sufficient condition for this is, indeed, that for all x,

$$k \leqslant \frac{\theta\alpha c_{x,k} - \lambda}{\theta\alpha c_{x,k} + \lambda}. \quad (15)$$

But from eqn (11) it follows that the right-hand side of the last inequality is a non-decreasing function of x, obtaining its minimal value $(\alpha\theta c - \lambda)/(\alpha\theta c + \lambda) = R$ at $x = x_1$. Hence, the requirement (i) for the stability of Γ_k against an intruder's over-aggression is satisfied if and only if

$$k < \frac{\theta\alpha c - \lambda}{\theta\alpha c + \lambda} = R, \tag{16}$$

R being, as we recall, the concord coefficient of the population, given in eqn (6).

By similar arguments the requirement (ii) for the stability of Γ_k against an owner's over-aggression is, therefore, satisfied if and only if

$$k > -\frac{\theta\alpha c - \lambda}{\theta\alpha c + \lambda} = -R. \tag{17}$$

From eqn (16) it follows, though, that no rule Γ_k is an ASS (hence, indeed no such rule can be an ESS) if $R < 0$. For $R \geqslant 0$, on the other hand, eqn (16) indeed implies eqn (17), hence it is a necessary and sufficient condition for ASS.

In Appendix B, we see that *inequality* (16) *is also a necessary and sufficient condition for the evolutionary stability of the strategy* Γ_k.

Employing this finding, one straightforwardly obtains the main result of this section.

Corollary. (a) *No natural priority rule is an* ASS, *notwithstanding an* ESS *if* $R < 0$ (*or, equivalently, if* $\lambda > \theta\alpha c$).

(b) *If* $R \geqslant 0$ *then the concord strategy* Γ_k *is an* ESS *for and only for* $k \leqslant R$.

(c) *If the Bourgeois Principle is an* ESS, *so is any alternative concord rule* Γ_k.

(d) *If some concord rule* Γ_k *is an* ESS, *then so must be the rule* Γ_0 *of strength-priority.*

(e) *If* $R = 0$ *then strength-priority is the only natural concord* ESS.

Remark. During the analysis of this section we have employed the probability $Q_k(x)$ that a potential intruder of body size x would ever get hold of a territory. Not surprisingly, it follows from eqns (11) and (12) that, except for the special case of the Bourgeois Principle, this probability depends on the distributions $G(x)$ of body size among owners. This, in turn, is most likely to depend on the population strategy Γ_k. (Indeed, if strength-priority prevails, larger individuals are more likely to be found among owners.) It is, therefore, important to notice that, except for the stability condition for the Bourgeois Principle, given in eqn (10), none of the results given in the corollary above depend on the distributions $G(x)$. Moreover, even the stability condition for the Bourgeois Principle depends only on the extremal values x_1 and x_2, which do not depend on the population strategy.

5. On the Failure of Concord Priority Rules and the Emergence of Partial Aggression—Why Low-rank Individuals are More Aggressive than High-rank Ones Toward their Inferiors?

Let us now assume $R < 0$. In such a case, we know that the Bourgeois Principle, even in its weak version Γ_k with any $k > 0$, cannot maintain in the population. We, therefore, restrict our attention now to strategies in which one's decision, either owner or intruder, is based exclusively on body size. We further assume that large individuals never yield to smaller ones, thus an aggressive confrontation occurs if and only if a smaller individual challenges a larger one. We shall refer to such strategies as *strength-oriented.* We now see that as the concord coefficient R does not drop too much below zero, the strength-priority rule remains in vigor among individuals above some critical size but not among smaller ones. When R drops further below zero, no individual in the population respects the strength-priority rule, at least when concerning opponents not too larger than himself.

Let the death intensity of a potential intruder of body size x, given a population strategy Γ, be $\lambda_\Gamma(x)$, death now resulting from either a natural cause or an aggressive confrontation. Also, let this individual's intensity of getting hold of a territory be $B_\Gamma(x)$. The probability that an x-size potential intruder will ever get hold of a territory before dying is, then

$$Q_\Gamma(x) = \frac{B_\Gamma(x)}{B_\Gamma(x) + \lambda_\Gamma(x)}. \tag{18}$$

Condition (3) for the advantage for an individual of body size x to yield to a larger opponent of body size $y > x$ can now be written as

$$Q_\Gamma(x) \geqslant \frac{p(x, y)}{\theta + (1-\theta)p(x, y)}. \tag{19}$$

Since $p(x, y)$ is a decreasing function of y, it follows from eqn (19) that if an individual yields to any specific opponent, he should indeed yield to any larger opponent. This means that any agent-stable strength-oriented strategy Γ can be characterized by a real function $y_\Gamma(x)$ such that for all $x_1 \leqslant x \leqslant x_2$, an individual of body size x would challenge opponents smaller than $y_\Gamma(x)$ and only such opponents. Differentiating eqn (19) with respect to x at the point $y = y_\Gamma(x)$, if it exists, we straightforwardly get, for any value $y > x$

$$y'_\Gamma(x) = \frac{[1-(1-\theta)Q_\Gamma(x)]p_x(x, y) - [\vartheta + (1-\theta)p(x,y)]Q'_\Gamma(x)}{[(1-\vartheta)Q_\Gamma(x) - 1]p_y(x, y)}.$$

However, it is easy to verify that at the point $x = y$, $p_y(x, y) = -p_x(x, y)$, hence, since $Q'_\Gamma(x) > 0$, we get

$$y'_\Gamma(x) = \left.\frac{[1-(1-\theta)Q_\Gamma(x)]p_x(x, y) - [\vartheta + (1-\theta)p(x, y)]Q'_\Gamma(x)}{[1-(1-\vartheta)Q_\Gamma(x)]p_x(x, y)}\right|_{y=x} < 1. \tag{20}$$

From eqn (20) it follows that the graph of $y_\Gamma(x)$ can intersect the main diagonal once at the most, within the interval $[x_1, x_2]$, say at the point x_Γ^*. If this occurs, we know that an individual of body size larger than x_Γ^* should respect the strength-priority rule, yielding to any larger opponent. An individual smaller than x_Γ^*, on the other hand, should challenge at least some opponents larger than him. If, on the other hand, no intersection x_Γ^* exists within the interval $[x_1, x_2]$, we know that any individual in the population should challenge at least some opponents larger than himself, the alternative that all individuals in the population respect the strength-priority rule being precluded by the assumption $R < 0$.

An individual of body size x respects the strength-priority rule if and only if, inequality (19) holds for all $y > x$. Out of continuity arguments, a necessary and sufficient condition for this is that eqn (19) holds for $x = y$. Recalling $p(x, x) = 1/2$, this yields

$$Q_\Gamma(x) \geqslant \frac{1/2}{\theta + (1-\theta)1/2} = \frac{1}{1+\theta}.$$

Inserting eqn (18) into this inequality, one can readily see that an individual of body size x would respect the strength-priority rule if and only if

$$\theta B_\Gamma(x) \geqslant \lambda_\Gamma(x). \tag{21}$$

Let us now concentrate on a potential intruder of the largest body size $x = x_2$ in the population. In addition to the intensity λ of natural death, such an individual can die only if defeated by a smaller challenging opponent. Denote

$$D_\Gamma = \int_{x_2 \leqslant y_\Gamma(\xi)} p(\xi, x_2)\,\mathrm{d}G(\xi). \tag{22}$$

This is the probability that, given the strategy Γ, a random owner in the population would challenge and defeat an intruder of size x_2. Since the intensity of finding a territory is α, since the probability of finding that territory occupied is $1 - c$, since the probability for an x_2-intruder to be challenged and defeated by the owner is D_Γ and since the conditional death probability, in such a case, is θ, we get

$$\lambda_\Gamma(x_2) = \lambda + \alpha\theta(1-c)D_\Gamma. \tag{23}$$

All the same, a potential intruder of body size x_2 would get hold of any territory he finds unless defeated by a smaller challenging opponent. In the same way as above, we now get

$$B_\Gamma(x_2) = \alpha[1-(1-c)D_\Gamma]. \tag{24}$$

Inserting eqns (23) and (24), condition (21) is satisfied for $x = x_2$ if and only if $\lambda \leqslant \theta\alpha[1 - 2(1-c)D_\Gamma]$. Employing eqn (6), this condition becomes

$$R \geqslant R_0, \tag{25}$$

where

$$R_0 = \frac{c - [1 - 2(1 - c)D_\Gamma]}{c + [1 - 2(1 - c)D_\Gamma]}. \tag{26}$$

But from eqn (22) it follows that $D_\Gamma = \int_{x_2 \leqslant y_\Gamma(\xi)} p(\xi, x_2)\,\mathrm{d}G(\xi) \leqslant \int_{x_1}^{x_2} p(\xi, x_2)\,\mathrm{d}G(\xi) < \frac{1}{2}$, hence $[1 - 2(1 - c)D_\Gamma] > c$. From eqn (26) it therefore follows that $R_0 < 0$ and we get the following corollary.

Corollary 5.1. (a) *A value $R_0 < 0$ exists, such that if $R_0 < R < 0$, then for any agent-stable strength-oriented strategy Γ, there is a critical body size x_Γ^*, $x_1 < x_\Gamma^* < x_2$, such that individuals above this critical value and only such individuals respect the rule of strength-priority.*

(b) *If $R \leqslant R_0$ then no individual in the population respects strength-priority, at least when facing individuals not too much larger than himself.*

The range of parameter $R_0 < R < 0$ appears to correspond to the common natural situation in which a strength-oriented concord resolution of conflicts prevails in most but not in all encounters. In such a case, we see that the population is divided into two well-defined ranks according to body size: an upper rank of individuals of body size $x > x_\Gamma^*$, and a lower rank of individuals of body size $x < x_\Gamma^*$. Corollary 5.1 asserts that strength-priority is globally respected only by individuals of the upper class. We now refer to the opposite question: The strength-priority of which individuals in the population is globally respected by all other individuals in the population?

We already know that for any agent-stable strength-oriented strategy, yielding to a given opponent implies yielding to any larger opponent. Less clear is the question under what condition being challenged by a given opponent implies being challenged by any larger one. It is easy to see, however, that this is the case if and only if, $y_\Gamma(x)$ is monotone increasing as a function of x. But the derivative of $y_\Gamma(x)$ is given by eqn (20) as one can easily verify, which is nonnegative if and only if

$$Q'_\Gamma(x) \leqslant \frac{2[1 - (1 - \theta)Q_\Gamma(x)]}{1 + \theta}\, p_x(x, y)|_{y = x}. \tag{27}$$

A counterexample to eqn (27) can be demonstrated (though for a limited range and with some technical difficulties) if, for example, $p_x(x, y)$ is sufficiently close to zero at some small enough vicinity of a given point $x = y = x_0$, assuming sufficiently high values elsewhere. Yet it appears that under most plausible regularity conditions, being challenged by one opponent implies being challenged by any larger opponent, in which case we speak of a *Regular Asymmetric Conflict*. For such conflicts we get the following corollary.

Corollary 5.2. *In any* ESS *of a regular asymmetric conflict*: (a) *If $R_0 < R < 0$ and $x_\Gamma^* < x < x_2$, then the strength-priority of an individual of size x is respected by all individuals of smaller body size.*

(b) *If $R_0 < R < 0$ and $x_1 < x < x_\Gamma^*$, then there are always individuals of body size smaller than x, that do not respect his strength-priority.*

(c) *If $R \leqslant R_0$, then no individual in the population totally respects the strength-priority.*

Proof. (a) If $R_0 < R < 0$ and $x_\Gamma^* < x < x_2$, then it follows from Corollary 5.1 that the strength-priority of the x-individual is respected by all individuals of body size y for which $x_\Gamma^* < y < x$. From the assumption of regularity it follows that the strength-priority of the x-individual is indeed respected by all individuals smaller than x_Γ^*.

(b) If $R_0 < R < 0$ and $x_1 < x < x_\Gamma^*$, or else if $R \leqslant R_0$, then it follows from Corollary 5.1 that $y_\Gamma(x) > x$. From the continuity of $y_\Gamma(x)$ it then follows that a value $\xi < x$ exists, for which $y_\Gamma(\xi) > x$, hence the strength-priority of x is not respected by ξ. □

Corollary 5.2 asserts that all aggressive confrontations in the population are expected to take place among individuals of the lower rank. Individuals of the upper rank, on the other hand, are never expected to fight, either with each other or with smaller individuals of the lower rank, the latter being expected to respect the strength-priority of the upper rank. In natural situations, however, upper-rank individuals with small differences in size are still likely, and in many populations are often observed, to maintain a sort of fake confrontation, in which a ritual pecking can serve to assure a recognized strength-priority. Lower-rank individuals, on the other hand, are likely to really fight to harm: a low-rank individual, when pecking a slightly inferior one, is not likely to do it in a ritual way, just to assure strength-priority, because such a priority is not expected to be recognized. Instead, it is in the best interest of the larger individual, in this case, to actually harm his inferior, who represents a permanent threat for him. Corollaries 5.1 and 5.2 can, therefore, provide a game-theoretical explanation, complementary to the ethological one, suggested by Lorenz (1963) for a wide variety of natural observations.

6. Summary and Discussion

In this work, we have studied a model for a population-game with multiple asymmetry. Individuals in the population were assumed to be different from one another with respect to two conspicuous factors: first, in some direct marker of strength, say body size, and then in their status as either an owner of a territory or a potential intruder. Concentrating on a situation in which ownership of a territory is a necessary condition for reproduction, it was assumed that natural selection operates to increase one's expected ownership-time.

The crucial parameters in the analysis of the model were the intensity λ of the natural-death event, the availability α of habitats, either empty or occupied, and the probability $c > 0$ that a habitat found is empty. If, on the other hand, a non-empty habitat is found, then both owner and intruder can each either yield or challenge. If both challenge, the winner takes over the habitat while the loser has a probability $0 < \theta \leqslant 1$ to die. It was further assumed that an individual of size x has a probability $p(x, y)$ to win a contest with an individual of size y, regardless of ownership. $p(x, y)$ was assumed to be a continuous increasing function of x and a continuous decreasing function of y, x_1 and x_2 being the body size of the smallest and the largest individual in the population, respectively.

We first ask about the conditions for the stability of the *Bourgeois Principle*, then for the existence of alternative stable concord strategies in the population. For this we have restricted our analysis to the so-called *natural rules* Γ_k ($k \geqslant 0$) of accepting the strength-priority when the difference in body size between opponents is sufficiently large, say $p(x, y) - p(y, x) > k$, and adopting the Bourgeois Principle otherwise. Stability, however, was checked against *any* alternative strategy. Finally, we have asked about the possible evolutionarily stable or at least agent stable strategies in a population under conditions which do not allow for any stable concord strategy. The main results of the model can be summarized as follows:

(a) The stability of the natural strategies of the population depends on a single parameter $R = (\alpha\theta c - \lambda)/(\alpha\theta c + \lambda)$, namely *the concord coefficient* of the owner–intruder conflict, R being an increasing function of the risk of conflict θ, and of the probability $\alpha c/(\alpha c + \lambda)$ of ever finding an empty habitat.

(b) If $R \geqslant p(x_2, x_1) - p(x_1, x_2)$, then the *Bourgeois Principle* of ownership-priority is evolutionarily stable, and so are all mixed natural priority rules Γ_k.

(c) If $0 \leqslant R < p(x_2, x_1) - p(x_1, x_2)$, then all natural priority rules Γ_k for which $0 \leqslant k \leqslant R$ and only these priority rules are evolutionarily stable.

(d) If $R = 0$, then the mere *strength-priority* Γ_0 is the only concord strategy which is evolutionarily stable.

(e) If $R < 0$, then no normal concord strategy can be evolutionarily stable or even agent-stable.

(f) A value $R_0 < 0$ exists such that if $R_0 < R < 0$ then agent-stable strategies (hence, evolutionarily stable strategies, if they exist) are characterized by the separation of the population into two distinct classes according to body size. Only individuals with body size above some critical value totally obey the rule of strength-priority. Under plausible assumptions it can be shown, moreover, that only the priority of these upper-class individuals is respected by all smaller individuals in the population.

(g) If $R \leqslant R_0$ then no agent-stable strategy (hence indeed, no ESS) determines full respect of strength priority by any individual in the population. Any individual in the population would then challenge a larger opponent if the difference in body size among them is not too large.

Starting our study in search of conditions for the stability of the Bourgeois Principle, condition (ii), given above, enables one to compare our results with those of previous models (Maynard Smith & Parker, 1976; Hammerstein, 1981; Grafen, 1987; Eshel & Sansone, 1995). Thus, in the case of no differences in body size, the condition for the stability of the Bourgeois Principle becomes $\alpha\theta c \geqslant \lambda$, which is, not surprisingly, the condition obtained in a previous work (Eshel & Sansone, 1995). More importantly, we see that this condition is not sensible for sufficiently small differences in body size, leaving the pure Bourgeois Principle evolutionarily stable. Moreover, even in a population with large differences in body size, as long as the condition $\alpha\theta c \geqslant \lambda$ for the stability of the Bourgeois Principle with the absence of strength-markers holds, the Bourgeois Principle was shown to remain a stable priority rule for encounters between opponents of limited difference in body size. Apparently, this could have justified as good approximation the previous life-history model in which differences in markers for strength were ignored. Unfortunately we know further, that whatever small differences in a direct strength-marker are introduced into the population, the Bourgeois Principle can well be replaced by pure strength-priority as well as by any Γ_k combination of the two, all being equally stable, once fixed in the population.

In likely natural situations, however, there is a crucial difference between the pure Bourgeois Principle and all other priority rules, concerning the accessibility of immediate information required for the contenders to follow them. While ownership is generally easy to recognize, it takes time for the contenders to estimate the values x and y of a strength-marker in real situations, a process that most often requires energy-consuming exhibitions and fake assaults. Moreover, the various parameters contributing to R are likely to fluctuate from time to time and place to place, rather than being fixed as in the model. It is, therefore, likely that, despite the array of alternative, potentially stable priority-rules, the Bourgeois Principle will be the first to establish itself whenever natural conditions enable its stability. Once destabilized due to environmental fluctuations, the Bourgeois Principle is likely to irreversibly be replaced by another priority rule. It is, therefore, expected that alternative priority rules, more biased toward strength, would be characteristic not only of harsh environments, but also of fluctuating ones.

In real situations, the Bourgeois Principle is likely to be characterized by quick resolution of the owner–intruder conflict, where at the appearance of the former, the latter immediately leaves the arena. This is not likely to occur in the case of other priority-rules, including those in which the Bourgeois Principle is partially in vigor, so that the observer can realize that in most cases it is the intruder that, after long or short display and negotiation, leaves the arena.

Once the Bourgeois Principle becomes unstable, it is not surprising that, as being shown in this work, the first to challenge it, thus giving room to multi-factor priority-rules, are potential intruders of large body size, when encountering owners of a sufficiently small body size. Strength or body size priority, on the other hand, is first challenged, as we have seen, by individuals of small body size, either owners or intruders, when they encounter opponents of slightly larger size. This finding can be explained by a variation of the *Desperado Effect*, suggested by Grafen (1987) with respect to potential intruders in a population governed by the Bourgeois Principle. In the case of strength-priority, it is the smallest individual in the population that, once losing a territory, may remain with little chance to ever get hold of one. Larger individuals can afford to wait for their turn.

This last finding has been suggested to account not only for the reluctance of low-rank individuals to accept the priority of slightly higher-in-rank opponents, but also for the aggression of low-rank individuals toward subordinates which are in a permanent threat for them (e.g. Lorenz, 1963).

Finally, it is worth noticing that none of the results mentioned depends on the distribution $F(x)$ of body size among potential intruders. This distribution indeed affects the length of time one is expected to hold a territory, if owner (depending on its body size) and, hence, the reproductive value of ownership. It does not affect the chance of a potential intruder of a given body size to ever get hold of a territory, whatever strategy it uses. Yet, in deciding whether to fight or to yield to a challenging opponent, one (either owner or intruder) can only weigh the appropriate chances of ending up holding a territory, either immediately or in the future. Such a decision is, therefore, independent of the actual reproductive value of ownership (as long as it is, indeed, positive) and, hence, of the distribution $F(x)$.

It was further shown that for $R \geqslant 0$, the stability of the concord strategies Γ_k is independent also of the distribution $G(x)$ of body size among owners (although the stability of the Bourgeois Principle does depend on the common support (x_1, x_2) of both $F(x)$ and $G(x)$. This is important because the strategy Γ_k itself may affect $G(x)$. Indeed, as the relative weight of strength-priority increases, smaller individuals are less likely to be found among owners.

This, however, is not true for the stable strength-oriented strategies studied under the assumption of $R < 0$, these strategies both depending on $G(x)$ and affecting it. Note, though, that the only results suggested in that section were, therefore, robustly independent of the specific distribution $G(x)$, assuming only its continuity.

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REFERENCES

ESHEL, I. & SANSONE, E. (1995). Owner–intruder conflict, Grafen effect and self-assessment: the Bourgeois principle re-examined. *J. theor. Biol.* **177**, 341–356.

ESHEL, I. & SHAKED, A. (2001). Partnership. *J. theor. Biol.* **208,** 457–474.

GRAFEN, A. (1987). The logic of divisively asymmetric contests: respect for ownership and the desperado effect. *Anim. Behav.* **35,** 462–467.

HAMMERSTEIN, P. (1981). The role of asymmetries in animal conflicts. *Anim. Behav.* **29,** 193–205.

LORENZ (1963). *On Aggression*. New York: Harcourt, Brace & World. [English translation 1966.]

MAYNARD SMITH, J. & PARKER, J. (1976). The logic of asymmetric contests. *Anim. Behav.* **25,** 1–9; *J. theor. Biol.* **25**, 93–101.

SELTEN, R. (1975). Reexamination of the perfectness concept for equilibrium points in extensive-form games. *Int. J. Game Theory* **4,** 25–55.

SELTEN, R. (1980). A note on evolutionary stable strategies in asymmetric animal conflicts, *J. theor. Biol.* **84,** 93–101.

APPENDIX A

The Bourgeois Principle is an ESS of the life-history model without body-size differences if eqn (5) holds and only if it holds at least as a weak inequality.

Proof. Denote here the Bourgeois Principle by BP. In Section 2, we have seen that a weak version of inequality (5) is a necessary condition for agent stability of BP, hence it is indeed a necessary condition for the evolutionary stability of it.

Suppose, on the other hand, that eqn (5) holds as a sharp inequality. If BP is not an ESS, then there must be an alternative strategy Γ, which is better than or equal to BP against BP. A Γ-strategist owner in a population fixed on BP would encounter only potential intruders that recognize its priority; hence, it can only lose by deviating from BP. Without loss of generality we can, thus, assume that the strategy Γ deviates from BP only with respect to the behavior of the potential intruder (otherwise we can replace Γ by an alternative strategy which is even better against BP). Being different from BP, the mutant strategy Γ should therefore determine a positive probability for the intruder to challenge an encountered owner.

Denoting by $T_1(\Gamma^1, \Gamma^2)$ the EOT of a potential Γ^1-intruder in a Γ^2-population, the requirement that Γ is better than or equal to BP against BP can be written as $T_1(\Gamma, BP) \geqslant T_1(BP, BP)$. We know though, that the EOT of a Γ and a BP-owner should be equal, say T_2. Denoting further by Q_Γ and Q_{BP} the probability that a Γ and a BP-intruder will ever get a hold of a territory, respectively, it follows from eqn (2) that

$$Q_\Gamma \geqslant Q_{BP}. \tag{A.1}$$

Since condition (5) guarantees that $Q_{BP} > p/[p + \theta(1 - p)]$, it follows that indeed

$$Q_\Gamma > \frac{p}{p + \theta(1 - p)}. \tag{A.2}$$

But inequality (A.2) is exactly the strict version condition for the advantage of a one-shot yielding for a potential Γ-intruder. In other words, given eqn (5), a potential Γ-intruder would strictly gain by replacing its strategy Γ by the non-stationary strategy $\Gamma^{(1)}$ of yielding in the first encounter and then, if remaining alive for the next one, continuing as a Γ-player, thus,

$$T_1(\Gamma^{(1)}, BP) > T_1(\Gamma, BP) \geqslant T_1(BP, BP). \qquad \text{(A.3)}$$

Denote now by $\Gamma^{(n)}$ the non-stationary strategy of yielding in the first n encounters and then, if remaining alive, continuing as a Γ-player. By iterating the single-shot argument given above, one infers that the sequence $\{T_1(\Gamma^{(n)}, BP)\}$ is strictly increasing. But for any $\varepsilon > 0$ there is a number n such that the probability of a potential intruder to remain alive and still potential intruder after n encounters is smaller than ε. Thus, the difference between $\Gamma^{(n)}$ and BP is restricted to an event of probability smaller than ε, and the difference in payoff, given this event, is bounded by T_2. Hence, we get

$$\lim_{n\to\infty} T_1(\Gamma^{(n)}, BP) = T_1(BP, BP) < T_1(\Gamma^{(1)}, BP). \qquad \text{(A.4)}$$

This stands in contradiction to the fact that sequence $\{T_1(\Gamma^{(n)}, BP)\}$ is a strictly increasing sequence. We thus conclude that under condition (5) the Bourgeois Principle (BP) is doing strictly better than any alternative strategy Γ against BP, hence, it is an ESS. □

APPENDIX B

If the priority rule Γ_k is an ASS, then it is also an ESS.

Remark. Here, in ESS we mean a strategy $\Gamma^{(1)}$ that, once fixed in the population, is immune to the invasion of any mutant strategy $\Gamma^{(2)}$ which, for any individual in the population, is *essentially different* from $\Gamma^{(1)}$. By "essentially different" we mean a strategy $\Gamma^{(2)}$ that, for any individual in the population, determines a behavior which is different on a set of positive probability from the one determined by the strategy $\Gamma^{(1)}$. Indeed, no strategy can possibly be immune to the invasion of alternative strategies that are not essentially different from it.

Proof. Assume that Γ_k is an ASS. Let us denote by $Q_\Gamma(x)$ the probability of a potential intruder of body size x and a strategy Γ ever to obtain a territory in a population fixed on the strategy Γ_k. If Γ_k is not an ESS, then there must be an essentially different strategy Γ that, for an individual of some body size x is at least as good as Γ_k against Γ_k. Without loss of generality, we can assume that $Q_\Gamma(x) \geqslant Q_{\Gamma_k}(x)$, otherwise, we can replace Γ by a strategy that is identical to Γ_k for the potential intruder and to Γ for the owner. That strategy would, indeed, be strictly better than Γ against Γ_k (hence, it should also be essentially different from Γ_k). In the same way, repeating the argument of Appendix A, we can assume, without loss of generality, that a Γ-player, either an owner or intruder, would stand its ground whenever its opponent yields, namely whenever a Γ_k-player stands its ground. But, Γ is assumed to be essentially different from Γ_k, it follows that for any body size x in the population, at least one of the two must hold:

(i) There is a positive probability that a Γ-intruder of body size x would challenge owners of body size y for which $p(x, y) - p(y, x) < k$.

(ii) There is a positive probability that a Γ-owner of body size x would challenge intruders of body size y for which $p(x, y) - p(y, x) < -k$.

In both cases the Γ-player would have to challenge a determined opponent in a situation in which we know that a Γ_k-player would not. Since Γ_k is an ASS, this means that yielding in these cases is indeed the best one-shot decision for the Γ_k-player. From eqns (3) and (13) it, therefore, follows that the values of y involved satisfy the inequality $Q_{\Gamma_k}(x) \geqslant p(x, y)/[p(x, y) + \theta p(y, x)]$ which is sharp for all but a zero-measure subset of values y. Having $Q_\Gamma(x) \geqslant Q_{\Gamma_k}(x)$, this indeed implies that in positive probability, a Γ-player of body size x would challenge an opponent of body size y for which

$$Q_\Gamma(x) > \frac{p(x, y)}{p(x, y) + \theta p(y, x)}. \qquad \text{(B.1)}$$

But from eqn (3) (see argument for eqn (13) above) it follows that eqn (B.1) guarantees the one-shot advantage for a Γ-player of body size x to yield to a determined opponent of body size y.

Now for a player of body size x, denote by $\Gamma_x^{(n)}$ the strategy of playing Γ_k at the first n encounters, then, if still alive, continuing according to Γ. As in the proof of Appendix A, the sequence $\{T_1(x, \Gamma_x^{(n)}, \Gamma_k)\}$ of EOT's of a potential intruder of body size x and strategy $\Gamma^{(n)_x}$ in a Γ_k-population, is strictly increasing. Yet as n tends to infinity, $T_1(x, \Gamma_x^{(n)}, \Gamma_k)$ tends, as before, to the value $T_1(x, \Gamma, \Gamma_k)$, which is strictly smaller than $T_1(x, \Gamma^{(1)}, \Gamma_k)$. This stands in contradiction with the finding that the sequence $\{T_1(x, \Gamma_x^{(n)}, \Gamma_k)\}$ is increasing. Γ_k is thus, strictly better against itself than any essentially different strategy Γ, hence it is an ESS.