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Owner-Intruder Conflict, Grafen Effect and Self-assessment. The Bourgeois Principle Re-Examined

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An owner-intruder conflict is analysed. While the Evolutionary Stable Strategies of both owner and intruder depend on the reproductive value of holding a territory or on the chance of getting one (Grafen, 1987), the values (and, therefore, the relevant payment functions of the relevant population game) depend on the population strategy. Conditions for observed, evolutionarily stable, mixed strategies are analysed.

1. Introduction

As first noted by Maynard-Smith & Parker (1976), there is a qualitative difference betwen Evolutionary Stable Strategies (ESSs) in symmetric and asymmetric population games. The first important example, was that of the well-known hawk-dove population game in which a player, when confronted with a random opponent, has to chose one of two possible strategies, that is whether to play a hawk or a dove (Maynard-Smith & Parker, 1976). While dove always yields to hawk and while two doves peacefully share the property, an encounter between two hawks is equally harmful to both. It is easy to see that in such a population game there is only one ESS and, with the high cost of a conflict, this ESS is always mixed.

As shown by Maynard-Smith & Parker, the situation is qualitatively different in the asymmetric case, in which encounters are held between opponents of two different status, one of which has a higher chance to win. An example of such an encounter is that of an owner-intruder conflict, in which it is supposed that the one who already holds the property shown by Maynard Smith & Parker, no mixed ESSs are possible in this type population game. In extreme cases, when the penalty for the loser is low relative to the value of the property in question, the only ESS solution is that of a pure hawk strategy. This is followed by both owner and intruder. Under a more plausible assumption there is, instead, a pure ESS in which one always plays hawk if owner, and dove if intruder. If this strategy is accepted by a large enough majority in the population, it is easy to see that any single player, either owner or intruder will lose if he plays differently. This ESS was called The Bourgeois ESS by Maynard-Smith & Parker. Surprisingly, if the asymmetry between owner and intruder is not too high, there is another pure ESS, namely the Paradoxical ESS, in which it is the intruder that plays hawk while the owner always yields. In any case, no mixed ESS exists in the owner-intruder conflict, however small the difference between the two. Even more surprising is that this remains true even if there is no difference at all between owner and intruder (except for their recognized identity as owner and intruder), a case in which the payment matrix of the asymmetric game is identical to that of the symmetric

As was later proved, more generally, no mixed ESS can possibly exist in any asymmetric, linear population game (Selten, 1980). This is one of the most fundamental and yet embarrassing results of population game theory. It will be dealt with in the second part of this work.

Concentrating on the special case of the owner-intruder conflict, it was further maintained by Maynard-Smith & Parker that the paradoxical ESS, when it exists, is not likely to be widely accepted in the population. They called the existence, under suitable conditions, of only one plausible ESS in which ownership is always respected without any aggressive conflict, the Bourgeois Principle. This principle has been suggested as a theoretical basis for the general analysis of animal behaviour in cases of territorial conflicts. As such, the Bourgeois Principle has been challenged by Grafen (1987) both on an empirical and a theoretical basis.

On the empirical level, it has been maintained by Grafen that Maynard-Smith & Parker based their theory on rather naive observations of territorial conflicts. Such observations, Grafen argued, tended to yield biased estimations of the level of aggressiveness. This is because, in contrast to the Grafen's interpretation, most observed encounters end up in a peaceful manner purely because they did not represent any real conflict to start with. Instead, they correspond to a situation in which a non-territorial individual (a potential intruder) is looking for an unoccupied territory. In doing so it shows himself, expecting the owner to do the same, if it exists. A real conflict occurs only when the non-territorial individual fails to locate an empty territory. But in this case, Grafen argues, the Bourgeois Principle, as suggested by Maynard-Smith & Parker, cannot possibly be applicable to the real situation because of a very simple theoretical reason: as long as the Bourgeois Principle is accepted by the potential intruder, it has virtually no chance whatsoever to ever get any territory of its own. In most real situations this means that it will have no chance to pass its genes to the next generation. A rebel non-territorial individual which refuses to accept the Bourgeois Principle, on the other hand, will have some chance. Hence natural selection must operate against acceptance of the Bourgeois Principle by non-territorial individuals.

Opposing the Bourgeois Principle of Maynard-Smith and Parker, Grafen (1987) suggested a contradictory principle, the Vagabond Principle, based on the observation that a non-territorial individual, when it comes to real conflict, has much less to lose in terms of potential fitness and it is,

What is a reasonable risk to be take
a non-territorial individual in its contest
territory? Grafen's criticism of the Bou
Principle was based on the claim that the
payment function of a non-territorial individual
be different from that of the territorial one
therefore, the two (or at least one of them) m
different from the standard payment fu
suggested by Maynard-Smith & Parker. But wh
the relevant payment functions to be used i
analysis of this case? The most reasonable a
suggested by Grafen, is the very chance to h
territory in the future or, better still (both for
and for intruder), the total length of time
expected to hold a territory in the futur
maintained by Grafen, this is, indeed, higher f
one which already holds a territory (the owner
for the one which does not and who, theref
willing to take a higher risk in order to get on
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relevant payment functions of the two p
involved in a specific encounter depend, in tu
the very strategy followed by other individuals
population, either owners or intruders (the
depend on many other fixed parameters tha
from one conflict to another). It is hard to fin
fault in Grafen's claim that, once the Bou
Principle is accepted in the population, the lif
potential intruder must be valued low, relative
value of the territory in contest. However,
another strategy becomes established in the
lation (as suggested by Grafen), this may not
any more.

This apparent paradox results from the
linearity of the population–game structure, in
as already maintained by Grafen, the pa
function itself depends on the population strat
this article we analyse such a nonlinear, asym
population game in which each player se
maximize the expected future time in which it
a territory until death. We see that, although S
theorem is not applicable to this sort
population–game, the results obtained are, q
ively, not very much different from the ones pr
by Maynard-Smith & Parker. The situat
different, as we see later, if we further assume,
more realistically, that individuals have some
information about their own physical situation
moment of the conflict and they can
accordingly. In this case, although some w
probabilistic version of the Bourgeois Princip
holds under certain conditions, there are
conditions that allow for a fully symmetric

2. Owner–Intruder Conflict: The General Model

We assume a large population in which each individual may be either an owner or a potential intruder. Potential intruders and owners are confronted at random, confrontation can occur at any infinitesimal time (dt), regardless of past history. As a result of a confrontation, owner and intruder can either switch roles, depart peacefully, in which case each remains in its previous role, or else one or two of them may die or be injured depending, at least statistically, on their strategies. Also, within this infinitesimal period of time, there is generally a positive probability that a potential intruder will obtain an unoccupied territory, or that it will die or that an owner will lose its property because of different reasons. In the most general case A_1dt and B_1dt are assigned to the probability that a potential intruder will get hold of a property and to the probability it will die, respectively, within the period of time dt. A_2dt and B_2dt are assigned to the probability that an owner will lose its property, staying alive or dying, respectively, during this time. Indeed, A_1, A_2, B_1 and B_2 depend on the strategies of both owners and intruders, although the way they depend on them are different from one ecological situation to another. In general we assume continuous ranges of variability for the strategies x and y assigned to intruders and owners respectively. We may interpret x and y as probability of acting hawk but they can have somehow different meanings. In any case, let $\hat{x}$ and $\hat{y}$ be an intruder's and an owner's strategy, respectively, adopted by the population, and let x and y be the appropriate strategies adopted by a mutant player, (employed within their possible interchanging roles). For a mutant, A_1 and B_1 depend only on x and $\hat{y}$ and not on $\hat{x}$ or y, because an (x, y)-intruder will never use the y-component of its strategy as long as it is not an owner and will never confront an $\hat{x}$-intruder during this period. By the same argument A_2 and B_2 depend on $\hat{x}$ and y alone. Intruders and owners may interchange roles during their lives and we assume that each of them seeks to maximize the time it holds a property, until death. This is the case when a property (say a territory or a mate) is the only means for reproduction. Denote by $T_1 = T_1(x, y; \hat{x}, \hat{y})$ and $T_2 = T_2(x, y; \hat{x}, \hat{y})$, respectively, the expected future ownership times (EFOT) for an (x, y)-individual which is, at the moment, a potential intruder and for one which is, at the moment, the owner of a property, when the population strategy is $(\hat{x}, \hat{y})$.

The EFOT of an individual at time t is equal to the period $(t, t + dt)$ plus the sum of its probabilities to be an owner and a surviving potential intruder at the end of this period, each multiplied by the appropriate EFOT T_1 and T_2.

For small dt, the expected ownership time within the period $(t, t + dt)$ will be $0 + o(dt)$ for a potential intruder and $dt + o(dt)$ for an owner.

Hence,

$$T_1 = (1 - A_1dt - B_1dt)T_1 + A_1dtT_2 + o(dt) \quad (1)$$

$$T_2 = dt + (1 - A_2dt - B_2dt)T_2 + A_2dtT_1 + o(dt) \quad (2)$$

as dt goes towards zero, one immediately gets:

$$(A_1 + B_1)T_1 = A_1T_2 \quad (3)$$

$$(A_2 + B_2)T_2 = 1 + A_2T_1. \quad (4)$$

Therefore,

$$T_1 = A_1/(A_1B_2 + B_1A_2 + B_1B_2) \quad (5)$$

$$T_2 = (A_1 + B_1)/(A_1B_2 + B_1A_2 + B_1B_2). \quad (6)$$

Note that the ratio between the loss of EFOT T_1 with the intruder's death and the value $(T_2 - T_1)$ in EFOT of winning a contest is $T_1/(T_2 - T_1) = A_1B_1^{-1}$.

As mentioned by Grafen (1987; see also Hammerstein and Richert, 1988), this value is not a constant as in the case of a Hawk-Dove game. Instead, both A_1 and B_1 depend on the mutant intruder's strategy x and on the population owner's strategy $\hat{y}$.

The situation can only be approximated by an asymmetric hawk-dove game if both the intruder's probability of death and its chance of gaining a new property, in a given time, are not affected much by either the intruder's or the common owner's strategy. This is the case when most properties are not occupied and, on the other hand, natural death, for example predation of potential intruders, is more common than owner-intruder confrontations (i.e. when those confrontations are not essential for the potential intruders' fitness; Grafen, 1987).

However, contrary to what is claimed by Grafen, this does not necessarily mean that in such cases (for example in the Maynard-Smith & Parker situation) fights will always be avoided when high risk. It is possible to think of a situation when predation of potential intruders is high and territories are hard to find. Assume that most territories are empty, hence confrontations are rare and $A_1B_1^{-1}$ does not change much with x and $\hat{y}$. In this case, the asymmetric hawk-dove model of Maynard-Smith & Parker is valid. Yet in the rare situation of a confrontation, both intruder and owner are likely to take high risks, new territory even though such territory, if found, is likely to be empty.

Alternatively, the 'Bourgeois Principle' can hold even when drastic changes of $A_1 B_1^{-1}$ with x and $\hat{y}$ occur.

PAYMENT FUNCTIONS AND SUPERIORITY OF INDIVIDUAL STRATEGIES

Suppose the population strategy is $(\hat{x}, \hat{y})$. Strategy (x', y) is superior, for the intruder mutant, over strategy (x, y) if, assigned its future strategy y as an owner,

$$T_1(x', y, \hat{x}, \hat{y}) > T_1(x, y, \hat{x}, \hat{y}).$$

Rewriting (5) as

$$T_1 = [B_2 + (A_2 + B_2)B_1/A_1]^{-1} \tag{5'}$$

and recalling that A_2, B_2 do not depend on x, it follows that the intruder's strategy x' is superior over x if and only if

$$A_1(x', \hat{y})B_1(x', \hat{y})^{-1} > A_1(x, \hat{y})B_1(x, \hat{y})^{-1} \tag{7}$$

regardless of y. Then rewriting (6) as

$$T_2 = [1 + A_1/B_1][A_2 + B_2 + B_2(A_1/B_1)]^{-1}, \tag{6'}$$

and recalling that $A_2, B_2 > 0$, it follows that, for any value of y (that is for any A_2, B_2), T_2 is increasing with A_1/B_1.

In the same way we say that a strategy (x, y') is superior over (x, y), given $(\hat{x}, \hat{y})$, for the owner if

$$T_2(x, y', \hat{x}, \hat{y}) > T_2(x, y, \hat{x}, \hat{y}).$$

From (6) it follows that (x, y') is superior for the mutant owner over (x, y) if and only if

$$B_1 A_2(y', \hat{x}) + (A_1 + B_1)B_2(y', \hat{x}) < B_1 A_2(y, \hat{x}) + (A_1 + B_1)B_2(y, \hat{x}) \tag{8}$$

where A_1, B_1 depend on x (and $\hat{y}$) but not on y.

But,

$$T_1 = T_2 A_1 (A_1 + B_1)^{-1}$$

therefore the ratio between T_1 and T_2 is independent of y (since A_1 and B_1 depend on x alone), hence a strategy (x, y'), which is superior for the owner over (x, y), is also superior for the intruder.

Note that while the superiority of (x', y) over (x, y) (for both owner and intruder) does not depend on y (but depends on $\hat{x}$ and $\hat{y}$), the superiority of (x, y') over (x, y) may depend on x. As a corollary we get:

Proposition 1. For any $\hat{x}$ and $\hat{y}$, both $T_1(x, y, \hat{x}, \hat{y})$ and $T_2(x, y, \hat{x}, \hat{y})$ are maximized at the same pair of values $(x, y) = (x^*, y^*)$.

Proof. The optimal value (or values) $x = x^*$ is Moreover, even if this optimal value is not uniq determines a unique (maximal) ratio A_1/B_1. Given value, any change of y which increases T_1, increases T_2 and vice versa, therefore, the opt value $y = y^*$ is also the same for T_1 and T_2.

Without loss of generality we can, therefore, s of $T_1(x, y, \hat{x}, \hat{y})$ as the payment function sought maximized by any individual in the population.

We are now looking for the ESS of the necessarily linear) population game determine the payment function T_1. Recall that a pair (is an ESS if and only if:

(i) $T_1(x, y, \hat{x}, \hat{y})$ is maximized at $(x, y) = (\hat{x}, \hat{y}$
(ii) if, for some $(\tilde{x}, \tilde{y})$, $T_1(\tilde{x}, \tilde{y}; \hat{x}, \hat{y}) = T_1(\hat{x}, \hat{y};$
then $T_1(\tilde{x}, \tilde{y}; \tilde{x}, \tilde{y}) < T_1(\hat{x}, \hat{y}; \tilde{x}, \tilde{y})$,

(see Maynard-Smith & Price, 1973; Maynard-Sm 1974).

Finally, we assume that A_i and B_i $(i = 1, 2$ differentiable. We know from (5′)

$$\text{sign}\, \partial T_1/\partial x = \text{sign}\{B_1 \partial A_1/\partial B_1/\partial x\}.$$

From (6′) we know

$$\text{sign}\, \partial T_1/\partial y = -\text{sign}\{B_1 \partial A_2/\partial y + (A_1 + B_1)\partial B_2/$$

Using these equalities, we attempt to charact corner and mixed equilibria, if they exist, in diff ecological situations of owner-intruder conflict.

3. The Maynard-Smith-Parker-Grafen Mode

In this model it is assumed that, in any infinites period of time dt, a potential intruder has a ch λdt to find a property, either occupied or empt proportion $0 \leqslant \nu < 1$ of the territories are empt which case the intruder becomes an owner wit any conflict. At the same time an owner has a ch μdt to be confronted by a potential intruder (μ i necessarily equal to λ since the number of occu territories is not likely to be equal to the numb individuals seeking a territory). Both intruder's owner's strategies are their probabilities, x an respectively, of fighting for a territory in cas confrontation, $0 \leqslant x, y \leqslant 1$. If they fight, the o wins with probability $0 \leqslant q \leqslant 1$, $(1 - q = p)$. winner of the conflict holds the territory. The dies with probability θ and becomes a pote intruder if it survives.

If only one of the contenders is willing to fig retains the property. If both are unwilling to then each of the contenders has a chance 0.5 to infinitesimal period dt, both owner and intruder have, respectively, a chance $\rho_2 dt$ and $\rho_1 dt$ of dying of natural reasons. We denote $r_2 = \rho_2/\mu$ and $r_1 = \rho_1/\lambda$. If $\rho_2 > 0$, v must be positive. In fact $v \geqslant \rho_2/(\rho_2 + \mu) = r_2/(r_2 + 1)$. Note that $r_2/(r_2 + 1)$ is the proportion of time in which a territory will be empty under the assumption of no new territories being available. We refer to the case $v = r_2/(r_2 + 1)$ as the case of a "saturated environment".

One easily calculates:

$$A_1 = \lambda\{v + (1 - v)[x(1 - \hat{y} + p\hat{y}) + (1 - x) \times (1 - \hat{y})/2]\} = \lambda\{v + 2^{-1}(1 - v)[1 - \hat{y} + (1 + (p - q)\hat{y})x]\} \quad (11)$$

$$B_1 = \rho_1 + \lambda(1 - v)\theta q x \hat{y} = \lambda\{r_1 + (1 - v)\theta q x \hat{y}\} \quad (12)$$

$$A_2 = \mu\{\hat{x}[1 - y(q + \theta p)] + 2^{-1}(1 - \hat{x})(1 - y)\} \quad (13)$$

$$B_2 = \mu[r_2 + \theta p \hat{x} y]. \quad (14)$$

From (9), it follows that:

$$\text{sign}\, \partial T_1/\partial x = \text{sign}\{r_1[1 + (p - q)\hat{y}]/2 - \theta q \hat{y}[2v + (1 - v)(1 - \hat{y})/2]\}\lambda^2(1 - v), \quad (15)$$

and we may prove:

Proposition 2. Neither ESS of the form $(\hat{x}, 0)$, nor of the form $(0, \hat{y})$, where $\hat{x}$, $\hat{y} < 1$, exist in the owner-intruder game with payment function T_1 (or T_2).

Proof. For $\hat{y} = 0$, sign $\partial T_1/\partial x =$ sign $\lambda r_1(1 - v)/2 > 0$ and, indeed, $x = 1$ is always the best intruder's reply against the owner's sure retreat. In the same way [from (10)] one can see that $y = 1$ is always the best reply against the intruder's strategy $\hat{x} = 0$.

For $\hat{y} = 1$ we get sign $\partial T_1(x, y, \hat{x}, 1)/\partial x = \text{sign}(pr_1 - qv\theta)$. Thus if

$$pr_1 < qv\theta \quad (16)$$

then $x = 0$ is the best reply against $\hat{y} = 1$. If the reverse of (16) holds, then $x = 1$ is the best reply against $\hat{y} = 1$. It is easy to see that, in this case, it is the best reply against any owner's strategy $0 \leqslant \hat{y} < 1$ (indeed, if fighting is always advantageous for the intruder even when the owner is surely going to defend its property, then it will be more advantageous to the intruder if the owner is going to defend its property only with probability $\hat{y} < 1$).

Although T_1 (the potential intruder's EFOT) at a random moment of no confrontation is not symmetrical in x and y (or in $\hat{x}$ and $\hat{y}$), the situation at a moment of decision making, say at the moment of confrontation, is absolutely symmetrical for owner and intruder, except for an exchange between p and q (if they are actually different). We therefore conclude that if

$$qr_1 < pv\theta \quad (17)$$

then $y = 0$ is the best reply against $\hat{x} = 1$ and, if the reverse of (17) holds, then $y = 1$ is the best reply against $\hat{x} = 1$. In this case it is also the best reply against any other intruder's population strategy.

Concentrating now on the four pure pairs of strategies (0, 0), (0, 1), (1, 0) and (1, 1), we conclude

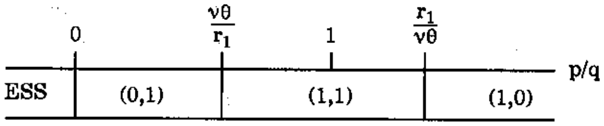
Proposition 3.

The pure ESSs of the model depend only on the relationship between the value $r_1/v\theta$ and the ratio p/q of the chances of the two opponents winning:

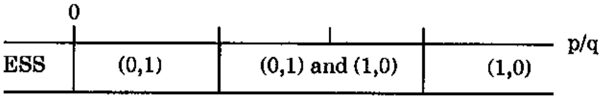
(i) if $q/p > r_1/v\theta > p/q$, then (0, 1) is the only ESS;
(ii) if $q/p < r_1/v\theta < p/q$, then (1, 0) is the only pure ESS;
(iii) if $q/p > r_1/v\theta < p/q$, then both (0, 1) and (1, 0) are ESS;
(iv) if $q/p < r_1/v\theta > p/q$, then (1, 1) is the only pure ESS.

Qualitatively, parts (i) and (ii) of Proposition 3 are

Case I. $\frac{r_1}{v\theta} > 1$



Case II. $\frac{r_1}{v\theta} < 1$



not surprising. As shown in Fig. 1, they only demonstrate that if one opponent (either the owner or the intruder) has a sufficiently larger chance of winning a fight, the other's best strategy is to always yield. More interesting is the dependence of the results on the value $r_1/v\theta$.

Recall that $r_1 = \rho_1/\lambda$, where ρ_1 is the intensity of natural death events among nomads. λv, on the other hand, is the intensity of nomad encounters with empty territories. The ratio $r_1/v = \rho_1/v\lambda$, is, therefore, the expected number of natural death events per any new colonization of an empty territory. It is called the cost of peaceful colonization, then

$$\frac{r_1}{v\theta} = \frac{\rho_1}{\lambda v\theta} = \frac{\text{the cost of peaceful colonization}}{\text{the cost of losing a fight}}$$

Now, having a chance p to win a fight, the expected gain of an intruder, if choosing to fight, is pr_1/v, while its expected loss is θq. In agreement with the verbal argument of Grafen (1987), it is expected that the intruder will always be willing to fight if, in doing so, its expected gain will be larger than its expected loss, namely $pr_1/v > \theta q$ or $r_1/v\theta > q/p$.

From the symmetry of the situation at the moment of the encounter, it follows that the condition $r_1/v\theta > p/q$ means that the expected gain of the owner, if choosing to fight, is larger than its expected loss in this case (here, gain and loss are measured in respect to the alternative of yielding and becoming a nomad).

Thus, not surprisingly, if both conditions are satisfied, say $q/p < r_1/v\theta < p/q$ (which is possible only in the case where $r_1/v\theta > 1$), both opponents will always choose to fight and (1, 1) is the only ESS.

If only one of the two conditions is satisfied, then the strongest opponent (for which, inevitably, the condition is satisfied) will always choose to fight and the other will always yield.

Finally, if none of the two conditions is satisfied, say if $q/p > r_1/v\theta < p/q$ (which is indeed possible only if $r_1/v\theta < 1$), both the Bourgeois solution (0, 1) and the Desperado solution (1, 0) will be ESSs: no opponent will be choosing to fight if the other one does.

In this case, what remains to be considered is the possibility of a fully mixed ESS $(\hat{x}, \hat{y})$ in which no opponent is fully bound to fight.

Note that the payment function T_1 (or T_2) is not a bilinear form of x, y, $\hat{x}$ and $\hat{y}$, hence Selten's Theorem precluding any mixed strategy does not apply here. Nevertheless, we get, in this model:

Proposition 4. No mixed ESS exists in the

Proof. A necessary condition for the ESS pro
of $(\hat{x}, \hat{y})$, when $0 < (\hat{x}, \hat{y}) < 1$, is

$$[\partial T_1(x, \hat{y}; \hat{x}, \hat{y})/\partial x]_{x=\hat{x}} = [\partial T_1(\hat{x}; y, \hat{x}, \hat{y})/\partial y]_{y=\hat{y}}$$

Employing (9) and (10), this becomes

$$B_1 A_1^{-1} = (\partial B_1/\partial x)(\partial A_1/\partial x)^{-1} \quad \text{at } (x, \hat{y}; \hat{x}, \hat{y})$$

and

$$(B_1 A_1^{-1})\partial(A_2 + B_2)/\partial y + \partial B_2/\partial y = 0 \quad \text{at } (\hat{x}, y;$$

Because A_1 and B_1 are linear functions of x a
independent of $\hat{x}$ and y, from (19), it follows
$B_1 A_1^{-1}$ is a function of $\hat{y}$ alone. A_2 and B_2 are
functions of $\hat{x}$ and y, independent of x and
follows from (20) and (19) that, for $(\hat{x}, \hat{y})$
satisfies (18), $B_1 A_1^{-1}(A_2 + B_2) + B_2$ is independe
either x or y. Using (5) we conclude that, for
which satisfies (18),

$$T_1(x, y; \hat{x}, \hat{y}) = [B_1 A_1^{-1}(A_2 + B_2) + B_2]^{-1} = T_1($$

(independently of x and y).

This means that for any $(x, y) \neq (\hat{x}, \hat{y})$:

$$T_1(x, y; \hat{x}, \hat{y}) = T_1(\hat{x}, \hat{y}; \hat{x}, \hat{y}).$$

But, from Proposition 3, we know that, for a
of parameters r_1, θ, p, v at least one of the pairs
(1, 0) and (1, 1) is a strict ESS, therefore if we c
(x, y) to be specific ESS, we get:

$$T_1(x, y; \hat{x}, \hat{y}) < T_1(x, y; x, y),$$

which, together with (22), means that $(\hat{x}, \hat{y})$ *is* n
ESS (see, for example Maynard-Smith, 1974
conclusion we get:

Proposition 5. The pairs (0, 1) (1, 0) and (1,
the only possible candidates for ESS. Proposit
gives the condition for the existence of all po
ESS of the system.

Note that in the proof of Proposition 4 we use
(9), (10), and the fact that A_1 and B_1 are
functions of x, independent on y, while A_2 and
linear function of y, independent on x.

In the symmetric case $p = q$, originally treat
Maynard-Smith & Parker, conditions (16) and
become identical and we get:

Proposition 6. In the symmetric owner-int
conflict, if

$$r_1/\theta v < 1$$

then the Bourgeois settlement (0, 1) and, theoreti
the alternative settlement (1, 0) are the only E

If the reverse of (24) holds then the only ESS is the total hawk solution (1, 1).

An unsurprising result, much in agreement with the verbal argument of Grafen (1987), is that in an unsaturated environment, when the availability v of free habitats is high, the Bourgeois Principle is most likely to be obeyed.

In case of saturated environment, where $v = r_2/(r_2 + 1)$, condition (24) becomes

$$r_1 < \theta r_2/(r_2 + 1). \tag{25}$$

If the death rate r_2 of owner is small, then this condition can be well approximated by

$$r_1/r_2 < \theta. \tag{26}$$

Thus, a necessary and sufficient condition for the Bourgeois Principle to be maintained in the population is, in this case, that the ratio between the death rates of the potential intruder and the owner will be less than the death probability of the loser.

An apparent discrepancy between the prediction of this model and what seems to be observed in natural situations is the failure of the model to predict any mixture of strategies. Considering Selten's theorem (1980), this is a general difficulty of population game theory when applied to asymmetric situations.

We therefore suggest two alternative models, within the general framework represented in Section 2. The first, ecogenetical model, presented in Section 4, takes into consideration the effect of the population strategy on the population density and, therefore, on the parameters μ and v. It sometimes allows for a mixed strategy to be adopted by one player (either intruder or owner). Yet the proof of Proposition 6 can be extended to this case and it does not allow for a fully mixed ESS.

In the second model we assume that individuals, either owners or intruders, are continually affected by many random factors, partly known to them but not to their opponents nor to the observer. The strategy of each individual is pure in the sense that it takes a probability-1 decision on the basis of many random factors, known only to it; to an observer, as well as to the opponent, it seems it takes a mixed strategy. Following Harsanyi (1973), we refer to such a strategy as a purified mixed strategy.

Following Maynard-Smith & Parker (1976) and Grafen (1987) we have assumed a so-called symmetrized model, that is one that becomes symmetrical with $p = 1/2$, at least at the moment of confrontation (a symmetrical version of the hawk-dove game). For this we have assumed, quite arbitrarily, that, in case confrontations, the goods of the property (namely the probability of ownership) are shared equally.

If we assume that, in this case, the property remains under the control of the owner, the structure analysed in Section 2 remains intact, and so do the death probabilities B_1 and B_2, as given by (12) and (14). However the probabilities A_1 and A_2 of status change, given by (11) and (13), respectively, should be replaced by

$$\tilde{A}_1 = \lambda\{v + (1 - v)x(1 - \hat{y} - p\hat{y})\} \tag{11'}$$

$$\tilde{A}_2 = \mu\hat{x}(1 - py - \theta qy) \tag{13'}$$

Since $\tilde{A}_1$ remains a linear function of x, independent of y, and $\tilde{A}_2$ remains a linear function of y, independent of x, the proof of Proposition 4 remains true. No mixed ESS $(\hat{x}, \hat{y})$ is allowed by this model. It is also easy to show that, as in the previous model, if $\hat{y} = 0$, $\partial T_1/\partial x > 0$ and, if $\hat{x} = 0$, $\partial T_1/\partial y > 0$, no ESS of the form $(0, \hat{y})$ or $(\hat{x}, 0)$ is possible. This leaves us with the cases in which either $\hat{x} = 1$, $\hat{y} = 1$ or both. From (11), (13) and (11′) and (13′) it follows that, in the specific cases $A_1 = \tilde{A}_1$ and $A_2 = \tilde{A}_2$, the two models become identical in respect to the predicted ESSs.

4. Ecogenetical Model

Dealing with the original Maynard-Smith-Parker-Grafen model (without self-assessment), we have seen that the structure of the population game depends on the parameters p, θ, ρ_1, ρ_2, λ and μ. In our analysis of the model we have assumed that these parameters are fixed, that they may affect the opponents strategies x and y but they are not affected by them. This is true by definition, for the natural death intensities ρ_1 and ρ_2. It is a most reasonable assumption for λ, the probability that a single wanderer finds a property, either occupied or empty, a factor which is not likely to be affected by the behavior of other individuals in the population. This assumption is more questionable when concerning μ, the intensity of potential invasions of a given habitat. This factor is likely to be proportional to the density of the potential intruder population. This density may decrease with the frequency of aggressive conflicts, which may end with death. However as μ decreases, $v = \rho_2(\rho_2 + \mu)^{-1}$ increases and the higher availability of empty habitats may decrease the incentive to resort to an aggressive solution.

The assumption that μ is a constant, independent of the population strategy is plausible in the situation of a large enough surplus of fertility, when the actual intruders is the carrying capacity of the land outside the main habitats under conflict.

In many cases it is more reasonable to assume a fixed flux of new recruits, say *hdt* individuals per habitat per an infinitesimal time interval *dt*. We assume that all new recruits start as potential intruders. At the same time interval *dt*, $[(1-\nu)\rho_2 + \mu\lambda^{-1}\rho_1]dt$ individuals per habitat in the population (either potential intruders or owners) die of natural causes, $\mu\lambda^{-1}$ being the number of potential intruders per habitat. Finally $\mu(1-\nu)xy\theta dt$ individuals per habitat die as a result of an aggressive conflict, $\mu(1-\nu)$ being the frequency of encounters per habitat, xy the relative frequency of aggressive conflict among them, θ the proportion of cases ending with death. Hence, in a stable situation

$$C = (1-\nu)\rho_2 + \mu\lambda^{-1}\rho_1 + \mu(1-\nu)xy\theta \qquad (27)$$

where

$$(1-\nu) = \mu(\rho_2 + \mu)^{-1}.$$

Denoting

$$c = C\rho_2^{-1}, \qquad (28)$$

$\nu = \nu(x, y)$ is the solution of

$$c = (1-\nu)\nu^{-1}[r_1 + \nu + (1-\nu)\theta xy]. \qquad (29)$$

At (0, 1), or at (1, 0) (29) becomes

$$c = (1-\nu)\nu^{-1}(r_1 + \nu). \qquad (30)$$

The right side of (30) is a decreasing function of ν. Using eqns (16) and (30), we know that a necessary and sufficient condition for the evolutionary stability of (0, 1) is

$$c < (p\theta - qr_1)(p\theta + q)(\theta pq)^{-1} = \hat{c}(r_1, p, \theta). \quad (31)$$

If $p\theta < qr_1$, (0, 1) is never evolutionarily stable (in this case it is worthwhile to attack rather than to wait for another encounter within a new habitat, even empty). If $p\theta > qr_1$, a low enough flux of new recruits guarantees the evolutionary stability of (0, 1). In the case $p = q$, cond. (31) becomes

$$c < (\theta - r_1)(\theta + 1). \qquad (32)$$

At (1, 1), on the other hand, eqn (29) becomes

$$c = (1-\nu)\nu^{-1}[r_1 + (1-\nu)\theta + \nu]. \qquad (33)$$

Again the right hand side is an increasing function of ν and the cond. (24) for the evolutionary stability of (1, 1) is

$$c = (p\theta - qr_1)[r_1\theta(p-q) + r_1 q + p\theta^2](r_1\theta pq)^{-1}$$

One can readily verify that for all $0 < r_1, \theta,$
$c^* > \hat{c}$, hence for $c^* > c > \hat{c}$ none of the corner
(0, 1) and (1, 1) are evolutionarily stable.

For example, if $p = q = 1/2$, $\theta = 1$ then

$$c^*(r_1, 1/2, 1) = (1 - r_1^2)r_1^{-1}$$

$$\hat{c}(r_1, 1, 1/2) = 2(1 - r_1)$$

with the ratio $c^*/\hat{c} = (1 + r_1)(2r_1)^{-1}$

By straightforward calculations one can sh
this case, if

$$2(1 - r_1) < c < (1 - r_1^2)r_1^{-1},$$

then both $(\hat{x}, 1)$ and $(1, \hat{x})$, where

$$\hat{x} = r_1[c - 2(1 - r_1)](1 - r_1^2)](1 - r_1^2)^{-1},$$

are ESSs.

It is easy to see that in this case $0 < \hat{x} < 1$ a
get a semi-mixed ESS in which one opponent
the owner or the intruder) always tends to fight
th other fights occasionally. Thus, if owners a
fight and intruders sometimes fight, intrude
indifferent towards fighting or not. Yet the sit
is stable because if intruders fought more there
be more deaths, a higher fraction of territories
be empty and so it would be advantageous not t
but to wait for an empty territory. Convers
intruders fought less than at ESS, there wo
fewer deaths, a smaller proportion of terr
would be empty, and so it would be advantage
fight. By symmetry we get another ESS in
intruders always fight and owners sometime do.
be shown, however:

Proposition. No fully mixed ESS $(\hat{x}, \hat{y})$ in
both $0 < \hat{x} < 1$ and $0 < \hat{y} < 1$ can exist i
ecogenetical model.

Proof. Since we accept the structure of Sect
and since A_1, B_1 are linear functions of x indepe
on y, since A_2, B_2 are linear functions
independent on x, the proof of Proposition 3 re
true.

5. Self-Assessment and Purified Mixed Strat

Natural conflicts are rarely fully symmetric
for examples Hammerstein, 1981). A careful ob
is likely to almost always find some, at least
asymmetry known to the contenders. The ana
the population game structure indicates that,
quite wide conditions, even the most minor
metry renders a mixed ESS impossible: for exa

game (Selten, 1980). It is also shown to be impossible in the nonlinear owner-intruder conflict analysed here. Yet what appears to be a mixed strategy is commonly observed in nature: it is rarely true that the owner always fights to defend its property (although it most often will) and it is even less common that the intruder either always yields or always fights.

Following Harsanyi (1973) in a different connotation, we believe that a common reason for the observed polymorphic behaviour is not the ubiquity of symmetric conflicts in nature but, on the contrary, the ubiquity of additional asymmetry, based on private information of each of the players. For example each player is likely to possess, at the moment of the conflict, some private information about its own resources or about other factors that affect its chance to win.

In this case it is reasonable that an individual decision to play hawk will not be random but will be based on its private information. Yet, since this information is hidden from either the opponent and from any observer, even a pure strategy as "to play hawk if own resources are above a given level" may be observed as a mixed strategy.

It would be preferable to speak in this case of an "observed-mixed strategy" but when there is no risk of confusion we speak simply of a "mixed strategy". A question raised by Harsanyi (1973) is what will be the limit-behaviour of this kind of mixed strategy (in his terminology of a "purified mixed strategy") when the effect of the private information on the actual outcome of the conflict tends towards zero.

Applying the assumption of private information to the case of owner-intruder conflict, we choose the simpler structure in which the time dependent "aptitude" ξ of the intruder and that, η, of the owner are each known to the player in question alone, $0 \leqslant \xi$, $\eta \leqslant 1$. A player's pure strategy, in this case, is to play hawk if and only if its aptitude is above a certain critical value (including the values 0, 1 which determine the players' observed "pure" strategies). Note that in this model we deal with a situation in which all players are of the same type. An individual's aptitude at the moment of any specific encounter is assumed to depend on temporal factors such as thirst, exhaustion and levels of energy which change from one encounter to the next.

Because of technical reasons we find it more convenient to deal with the values $X = 1 - \xi$, $Y = 1 - \eta$. A typical pure intruder's strategy x and a typical owner's pure strategy y is to play hawk if their private values X and Y at the time of confrontation are below x and y, respectively. In a way consistent

$y = 0$) means "to never play hawk" while $x = 1$ (or $y = 1$) means "to always play hawk".

We assume that the chance that an opponent (either intruder or owner) with a private "weakness" value x will win a conflict with an opponent with a "weakness" value y is $\phi(x - y)$, where $\phi'(s) < 0$ for all $0 \leqslant s < 1$ and $\phi(-s) = 1 - \phi(s)$. In the general case one of the two opponents (probably the owner) is likely to be of higher aptitude and more likely to win. In this case, the distribution of the private information value X of the intruder, say F_1, and that of the private information value Y of the owner, say F_2, may be different. Following both Maynard-Smith & Parker and Grafen models, we concentrate only on the interesting case of a symmetrical distribution $F_1 = F_2 = F$, that is the case in which, using the notation of Hammerstein (1981), ownership is "payment and outcome irrelevant".

It is not surprising that in this model one is likely to find so-called observed-mixed strategies. What remains to be considered, though, is the more crucial question of how much will the ESSs of the model still depend on ownership.

More specifically, assume that $(\hat{x}, \hat{y})$ is an observed-mixed ESS (that is such that $0 < F(\hat{x}) < 1$, $0 < F(\hat{y}) < 1$). We say that it follows the Weak Bourgeois Principle if $\hat{x} < \hat{y}$ (if the owner is more willing to play hawk).

We now show that, under quite plausible conditions, in addition to the weak Bourgeois ESS, there always exists a symmetric ESS $(\hat{x}, \hat{x})$ in which ownership plays no role in the decision of the players.

Assuming the case $F_1 = F_2$ in which ownership is payment-irrelevant, it is convenient to map the "individual aptitude" parameters, in a monotone way, on the interval [0, 1] such that X will be uniformly distributed on this interval. Hence, without loss of generality, one can assume

$$F(u) = \begin{cases} 0, \text{ if } u < 0 \\ u, \text{ if } 0 \leqslant u \leqslant 1 \\ 1, \text{ if } u > 1. \end{cases} \tag{37}$$

With this assumption, for any $0 \leqslant x, y \leqslant 1$, we denote by

$$\Delta(x, y) = \int_0^y \int_0^x \phi(u - v)\, \mathrm{d}F(u)\, \mathrm{d}F(v) \tag{38}$$

the probability that, in a confrontation between an x-strategist and a y-strategist, an actual contest will chance of an actual contest in which the y-strategist wins is

$$\Delta(y, x) = \int_0^y \int_0^x \phi(v-u)\, \mathrm{d}F(u)\, \mathrm{d}F(v) =$$

$$\times \int_0^y \int_0^x [1-\phi(u-v)]\, \mathrm{d}F(u)\, \mathrm{d}F(v)$$

$$= xy - \Delta(x, y) \tag{39}$$

and it follows from equality (38) and (39) that

$$\Delta(x, x) = x^2/2. \tag{40}$$

Using the notation of equal (38) one readily gets

$$A_1 = \lambda v + \lambda(1-v)[(1+x)(1-\hat{y})/2 + \Delta(x, \hat{y})]. \tag{41}$$

This is so because at any infinitesimal time-interval of length dt, a potential intruder has a chance $\lambda v dt$ to find an empty property and to become an owner without any conflict. It has a chance $\lambda(1-v)\,dt$ to find an occupied territory, in which case it may still become owner either with or without a real contest. First there is a probability $x(1-\hat{y})$ that the owner (which must be a conservative $\hat{y}$-strategist) will not play hawk but the intruder will, in which case the intruder gets the property without a fight. Then there is the probability $(1-x)(1-\hat{y})$ that neither are willing to fight, in which case it has been assumed that each has a probability 1/2 to get hold of the property, regardless of previous ownership. The general chance of getting hold of an occupied territory without a fight is

$$x(1-\hat{y}) + (1-x)(1-\hat{y})/2 = (1+x)(1-\hat{y})/2.$$

The chance of getting the property as a result of a fight is, by definition, $\Delta(x, \hat{y})$ and we get the (41).

In the same way, a potential intruder has a chance $r_1\lambda$ to die naturally during a time-period of length dt and has a chance $\lambda(1-v)\Delta(\hat{y}, x)\,dt$ to find an occupied territory, to fight and to lose during this time period, in which case it has a chance θ to die. Using equality (39) we get

$$B_1 = \lambda r_1 + \lambda(1-v)\theta[x\hat{y} - \Delta(x, \hat{y})]. \tag{42}$$

In the same way one can easily calculate

$$A_2 = \mu(1-y)(1+\hat{x})/2 + \mu(1-\theta)\Delta(\hat{x}, y), \tag{43}$$

and

Denote

$$g(x, y) = \partial\Delta(x, y)/\partial x = \int_0^y \phi(x-v)\, \mathrm{d}F(v),$$

we readily get from (39) and (45)

$$\partial\Delta(x, y)/\partial y = \int_0^x \phi(u-y)\, \mathrm{d}F(u) = x - g(y, x).$$

Using this notation, it follows from equalitie
and (42) that

$$\partial A_1/\partial x = \lambda(1-v)[(1-\hat{y})/2 + g(x, \hat{y})],$$

$$\partial B_1/\partial x = \lambda\theta(1-v)[\hat{y} - g(x, \hat{y})].$$

From (43) and (44) it follows that

$$\partial A_2/\partial y = -\mu\{(1+\hat{x})/2 - (1-\theta)[\hat{x} - g(y, \hat{x})]$$

$$\partial B_2/\partial y = \mu\theta[\hat{x} - g(y, \hat{x})].$$

Now, for any population strategy $(\hat{x}, \hat{y})$, v
interested in the "reply strategy" $(\tilde{x}, \tilde{y})$
maximizes the individual payment $T_1(x, y$
against this population strategy. We are speci
interested in those population strategies $(\hat{x}, \hat{y})$
are strictly the best replies against themselves,
in the strict ESSs of the population game.

More specifically we are interested in str
$(\hat{x}, \hat{y})$ which, at $x = \hat{x}$, $y = \hat{y}$ satisfy the followi
conditions:

$$\frac{\partial T_1}{\partial x} = 0$$

$$\frac{\partial T_1}{\partial y} = 0$$

$$\frac{\partial^2 T_1}{\partial x^2} < 0$$

$$\frac{\partial^2 T_1}{\partial y^2} < 0$$

and

$$\frac{\partial^2 T_1}{\partial x^2}\frac{\partial^2 T_1}{\partial y^2} - \left(\frac{\partial^2 T_1}{\partial x \partial y}\right)^2 > 0.$$

Recalling (see Section 2) that A_1 and
functions of x and $\hat{y}$ alone and that A_2 and
functions of $\hat{x}$ and y alone we employ conds.
(10) to get

$$\operatorname{sign}\frac{\partial T_1}{\partial x} = \operatorname{sign}\frac{\partial}{\partial x}\left(\frac{A_1}{B_1}\right) = \operatorname{sign}\{B_1 \partial A_1/\partial x$$

$$\operatorname{sign}\frac{\partial T_1}{\partial y} = \operatorname{sign}\{-B_1(\partial A_2/\partial y + \partial B_2/\partial y) - A_1\partial B_2/\partial y\}. \quad (57)$$

We are first looking for a symmetric ESS $\hat{x} = \hat{y}$, if it exists. Thus, at $x = y = \hat{x} = \hat{y}$,

$$\partial A_1/\partial x = \lambda(1-\nu)[(1-x)/2 + g_x],$$

where $g_x = g(x, x)$

$$\partial A_2/\partial y + \partial B_2/\partial y = -\mu[(1-x)/2 + g_x],$$

thus

$$\lambda(1-\nu)(\partial A_2/\partial y + \partial B_2/\partial y) = -\mu\partial A_1/\partial x,$$

$$\partial B_1/\partial x = \lambda\theta(1-\nu)(x - g_x),$$

$$\partial B_2/\partial y = \mu\theta(x - g_x),$$

hence

$$\lambda(1-\nu)\partial B_2/\partial y = \mu\partial B_1/\partial x$$

and we get:

$$\mu\{B_1\partial A_1/\partial x - A_1\partial B_1/\partial x\} = \lambda(1-\nu) \times\{-B_1(\partial A_2/\partial y + \partial B_2/\partial y) - A_1\partial B_2/\partial y\}. \quad (58)$$

Thus, from equality (56)–(58) it follows that, at $x = y = \hat{x} = \hat{y}$,

$$\operatorname{sign}\partial T_1/\partial x = \operatorname{sign}\partial T_1/\partial y = \operatorname{sign} L(x) \quad (59)$$

where

$$L(x) = \mu(B_1\partial A_1/\partial x - A_1\partial B_1/\partial x)/\lambda(1-\nu) = \{[r_1 + (1-\nu)\theta x^2/2][(1-x)/2 + g_x] - (\nu+1)\theta(x - g_x)/2\}\lambda\mu \quad (59')$$

From def (45) it follows that $g_0 = g(0, 0) = 0$ hence immediately it yields

$$L(0) = r_1/2 > 0. \quad (60)$$

On the other hand, since

$$g_1 = g(1, 1) = \int_0^1 \phi(1-\nu)\,\mathrm{d}F(\nu) > 0, \quad (61)$$

we get

$$L(1) = \lambda\mu[-\theta(1+\nu)/2 + (r_1 + \theta)g_1]. \quad (62)$$

Hence:

Proposition 7. If

$$\theta(1+\nu)$$

or, equivalently, if

$$r_1 < \frac{\theta(1+\nu-2g_1)}{2g_1} = r_1^*, \quad (64)$$

then $L(1) < 0$ and it follows from (60) and (62) that the equation $L(x) = 0$ has at least one solution $x = x^*$ at which

$$\frac{\partial T_1}{\partial x} = \frac{\partial T_1}{\partial y} = 0, \quad \text{at} \quad x = y = \hat{x} = \hat{y} = x^*.$$

In this case equalities (51) and (52) are simultaneously satisfied.

Note that, from (61), g_1 is the chance that an individual in its weakest possible situation $x = 1$ (according to its personal knowledge) will win a fight against a random opponent. We have $0 \leqslant g_1 \leqslant 1/2$, where $g_1 = 1/2$ is possible only in the extreme situation in which the personal knowledge x of the individual's state does not have any effect on the outcome of the fight. On the other hand, $g_1 = 0$ represents the other extreme situation, namely that of the strongest possible dependence of the outcome of the fight on the personally known state x. In this situation, being at the state $x = 1$, the individual has no chance to win a fight against any opponent.

More generally, a small value of g_1 can be interpreted as a strong dependence of the outcome of the fight on personal knowledge of one's own situation. Thus the condition (63) for the simultaneous satisfaction of equalities (51) and (52) requires strong dependence of the outcome of the fight on private personal knowledge.

The equivalent condition (64) requires that the natural death rate r_1 among potential intruders will be sufficiently low, depending on g_1. But the critical value r_1^*, as given by cond (64), is a decreasing function of g_1 and, as $g_1 \leqslant 1/2$ (being equal to 1/2 only if the winning chance of the weakest is equal 1/2 as that of any other individual), we get

$$r_1^* = r_1^*(\theta, \nu, r_1) > r_1^*(\theta, \nu, 1/2) = \nu\theta. \quad (65)$$

Thus, a sufficient condition for the simultaneous satisfaction of (51) and (52) is $r_1 < \nu\theta$.

Quite surprisingly, this is exactly the condition (24) for the Bourgeois pair of strategies (0, 1) to be an ESS in the Maynard-Smith-Parker-Grafen model.

We now prove the main result of this section, namely that, at $x = y = \hat{x} = \hat{y} = x^*$, a simultaneous satisfaction of equalities (51) and (52) implies the inequality (53–55). Thus, if $x = x^*$ is the solution of $L(x) = 0$, the pair $(x, y) = (x^*, x^*)$, at least locally, maximizes the value of $T_1(x, y, x^*, y^*)$ and it is, First we employ (5) to show

$$\frac{\partial^2}{\partial y^2}\left(\frac{1}{T_1}\right) = \left(1 + \frac{B_1}{A_1}\right)\frac{\partial^2 B_2}{\partial y^2} + \frac{B_1}{A_1}\frac{\partial^2 A_2}{\partial y^2} \tag{66}$$

(since A_1 and B_1 are independent on y).

But, from (49), it follows that

$$\frac{\partial^2 A_2}{\partial y^2} = -(1-\theta)\mu\frac{\partial g(y,\hat{x})}{\partial y} \tag{67}$$

while, from (50), we get

$$\frac{\partial^2 B_2}{\partial y^2} = -\theta\mu\frac{\partial g(y,\hat{x})}{\partial y}. \tag{68}$$

From conds (66) and (68) we get

$$\operatorname{sign}\frac{\partial^2}{\partial y^2}\left(\frac{1}{T_1}\right) = -\operatorname{sign}\frac{\partial g(y,\hat{x})}{\partial y}$$

$$= -\frac{\partial}{\partial y}\int_0^{\hat{x}} \phi(y-u)\,\mathrm{d}F(u)$$

$$= -\int_0^{\hat{x}} \phi'(y-u)\,\mathrm{d}F(u)$$

$$= \phi(y) - \phi(y-\hat{x}) > 0 \tag{66'}$$

(since $\phi(u)$ is a decreasing function of u).

Hence from (52) and (66′) it follows that at $x = y = \hat{x} = \hat{y} = x^*$, as

$$\frac{\partial T_1^{-1}}{\partial y} = 0,$$

we get:

$$\frac{\partial^2 T_1}{\partial y^2} = -T_1^2\frac{\partial^2}{\partial y^2}\left(\frac{1}{T_1}\right) < 0$$

which completes the proof of inequality (54).

Now (53) is proved by symmetry: we know that, given $\hat{x}$ and $\hat{y}$, T_1 and T_2 obtain their maximum (either as a function of x or of y) at the same values, thus, as a result of (54), we know that $T_2(x, y; x^*, y^*)$ and $T_1(x, y; x^*, y^*)$ obtain a strict local maximum at $y = x^*$. This means that at any encounter between an intruder and an owner, when the population strategy is (x^*, x^*), $y = x^*$ is the best owner's strategy, at least in the vicinity of x^*, assuming that it is also the strategy of its random opponent. But at the moment of the encounter, the situation is symmetrical in the sense that the future payment function of each is not (provided each keeps its original strategy). Ther at least locally, $x = x^*$ is also the best intr strategy, given it is encountering a random ow an (x^*, x^*) population. Thus, $T_1(x, y; x^*, y^*)$ o a local strict maximum at $x = x^*$; a condition is (53). But from (59) and (59′) it follows th $x = y = \hat{x} = \hat{y}$, (54) is equivalent to (53) and on remains to be proved. In order to prove this, the fact that since $x = y = \hat{x} = \hat{y}$, $T_1 >$ $(\partial T_1/\partial x) = (\partial T_1/\partial y) = 0$, we have $(\partial T_1^{-1}/\partial x) =$ $\partial y) = 0$.

But

$$\frac{\partial^2 T_1}{\partial x \partial y} = \frac{\partial^2}{\partial x \partial y}\left(\frac{1}{T_1}\right)^{-1} = \Bigg[2T_1\frac{\partial}{\partial x}\left(\frac{1}{T_1}\right)\frac{\partial}{\partial y}\Bigg(\frac{1}{T_1}$$

$$-\frac{\partial^2}{\partial x \partial y}\left(\frac{1}{T_1}\right)\Bigg]T_1^2 = -T_1^2\frac{\partial^2}{\partial x \partial y}\Bigg($$

Employing (5) we get, then,

$$\frac{\partial^2 T_1}{\partial x \partial y} = -T_1^2\frac{\partial^2}{\partial x \partial y}[B_2 + (A_2 + B_2)(B_1 A_1^{-1})$$

$$= -T_1^2\frac{\partial}{\partial y}(A_2 + B_2)\frac{\partial}{\partial x}\left(\frac{B_1}{A_1}\right)$$

since A_2 and B_2 are independent on x and A_1 are independent on y. But from (9) we kno $\operatorname{sign}(\partial T_1/\partial x) = \operatorname{sign}\partial(B_1 A_1^{-1})/\partial x$, so, at the $x = y = \hat{x} = \hat{y} = x^*$, $\partial(B_1 A_1^{-1})/\partial x = 0$. It f from (69) that $\partial^2 T_1/\partial x \partial y = 0$ and (55) f immediately from (53) and (54).

In this way we have proved that, at a so $x = x^*$ of $L(x) = 0$, conds (51–55) are satisfied (x^*, x^*) is a local strict ESS, that is whe established in the population it is stable a against small enough deviations from it (see 1982).

From this and from Proposition 7 we get:

Proposition 8. Under the condition (63) o with any value of $0 \leqslant g \leqslant 1$, there is a local symmetric ESS (x^*, x^*) in which the infor about previous ownership becomes irrelevant

We refer to such an ESS as an observed non-Bourgeois ESS and we have proved its ex under the condition (64) which, except for th $g_1 = 1/2$, is strictly weaker than (24). If, on th hand, the reverse of (64) is satisfied, then we that $L(1) > 0$ or

$$\partial T_1 > 0, \quad \text{for all } 0 \leqslant x \leqslant 1.$$

Inequality (70) means that, in this case, the total hawk strategy $(\hat{x}, \hat{y}) = (1, 1)$ is, at least locally, a strict ESS. It occurs, when r_1 is large enough (in fact larger than the requirement for such a solution without private information) and it is less likely to occur as g_1 becomes substantially smaller than 1/2 (that is as the private information becomes more important to the result of the fight). It never happens, regardless of r_1, if $g_1 = 0$.

In this case we get

Proposition 9. If a non-symmetric (non-Bourgeois) mixed ESS exists [that is if the reverse of (64) holds] then the total hawk strategy (1, 1) is a strict, local, ESS.

We can summarize that, in the case of private information (regardless of how important it is to the outcome of the actual conflict), a symmetric non-Bourgeois ESS, either "observed-mixed" or "pure" (total hawk) always exists.

6. Non-symmetric ESS's of the Purified Model

We now show that the symmetric, non-Bourgeois ESS, when it exists, is not necessarily the only ESS allowed by the conflict. We first study the condition for the existence of a (pure) Bourgeois ESS $(\hat{x}, \hat{y}) = (0, 1)$. (Note, however, that when such an ESS exists then by symmetry the Desperado ESS $(1, 0)$ exists as well). More specifically we are interested in the condition under which, for all $(x, y) \neq (0, 1)$

$$T_1(0, 1; 0, 1) > T_1(x, y; 0, 1). \qquad (71)$$

First, if $\hat{x} = 0$ it follows immediately from (39) that $\Delta(\hat{x}, y) = \Delta(0, y) = 0$. In this case, (43) and (44) become

$$A_2 = \mu(1 - y)/2 \qquad (43')$$

$$B_2 = \mu r_2. \qquad (44')$$

Hence:

$$T_1(x, y; 0, \hat{y}) = [B_2 + (A_2 + B_2)(B_1 A_1^{-1}]^{-1}$$
$$= [\mu r_2 + \mu(r_2 + (1 - y)/2)(B_1 A_1^{-1})]^{-1}.$$

This is an increasing function of y regardless of x and $\hat{y}$ (which, in turn, determines A_1 and B_1). As a special case it is true for $\hat{y} = 1$. Thus, for all x and y, we obtain

$$T_1(x, 1; 0, 1) > T_1(x, y; 0, 1) \qquad (72)$$

But, for $\hat{y} = 1$, (38) becomes

$$\Delta(x) = \Delta(x, 1) = \int^{1} \int^{x} \phi(u - v)\, \mathrm{d}u\, \mathrm{d}v. \qquad (73)$$

Employing (45) we get

$$\Delta'(x) = \int_0^1 \phi(x - v)\, \mathrm{d}F(v) = g(x, 1) \qquad (74)$$

and (since ϕ is a decreasing function)

$$\Delta''(x) = g'(x, 1) = \int_0^1 \phi'(x - v)\, \mathrm{d}F(v) = \phi(x)$$
$$- \phi(x - 1) < 0 \qquad (75)$$

which means $g'(x, 1) < 0$.

Thus for $\hat{y} = 1$, (41) and (42) yield:

$$A_1 B_1^{-1} = \frac{\nu + (1 - \nu)\Delta(x)}{r_1 + (1 - \nu)\theta[x - \Delta(x)]}; \qquad (76)$$

from (9) and (76) we then get:

$$\operatorname{sign} \frac{\partial T_1}{\partial x} = \operatorname{sign} \frac{\partial}{\partial x} \frac{A_1}{B_1} = \{r_1 + (1 - \nu)$$
$$\times \theta[x - \Delta(x)]\} g(x, 1)$$
$$- \theta[1 - g(x, 1)][\nu + (1 - \nu)\Delta(x)]; \qquad (77)$$

$$\operatorname{sign} \frac{\partial^2 T_1}{\partial x^2} = \operatorname{sign} \frac{\partial^2}{\partial x^2} \frac{A_1}{B_1} = [r_1 + \nu\theta$$
$$+ \theta(1 - \nu)x] g'(x, 1) < 0; \qquad (78)$$

this is true for $\hat{y} = 1$ and for any value of x, y and $\hat{x}$.

As a special case it is true for $\hat{x} = 0$, $y = \hat{y} = 1$. Thus, from the concavity property (78) of $T_1(x, 1; 0, 1)$ it follows that if $\partial T_1/\partial x < 0$ at $x = 0$, it is negative for all x. In this case $T_1(x, 1; 0, 1) < T_1(0, 1; 0, 1)$ for all x and from cond (66′) it follows that, for all $(x, y) \neq (0, 1)$, $T_1(x, 1; 0, 1) > T_1(x, y; 0, 1)$ which is exactly the requirement for the ESS property of (0, 1).

If, on the other hand, $[\partial T_1(x, 1; 0, 1)/\partial x]_{x=0} > 0$, then for some values of x, close to 0 and for $y = 1$, (71) cannot possibly be satisfied. A necessary and sufficient condition for (71) is

$$\left[\frac{\partial T_1(x, 1; 0, 1)}{\partial x}\right]_{x=0} < 0. \qquad (79)$$

But, at $x = 0$ it follows from (73) that

Employing the notation (45) and using the symmetry of F we get:

$$g(1,1)=\int_0^1 \phi(1-v)\,\mathrm{d}F(v)=-\int_0^1 \phi(1-v)\,\mathrm{d}F(1-v)$$

$$=-\int_0^1 \phi(v)\,\mathrm{d}F(v),$$

hence, because of the requirement $\phi(-u) = 1 - \phi(u)$, we get:

$$g(0,1)=\int_0^1 \phi(-v)\,\mathrm{d}F(v)=\int_0^1 [1-\phi(v)]\,\mathrm{d}F(v)$$

$$=1-\int_0^1 \phi(1-v)\,\mathrm{d}F(v)=1-g(1,1)$$

$$=1-g_1. \tag{81}$$

Inserting equalities (80) and (81) in (77) we get

$$\left[\frac{\partial T_1(x,1;0,1)}{\partial x}\right]_{x=0} = r_1(1-g_1)-v\theta g_1. \tag{82}$$

The condition (79) for the evolutionary stability of the pure Bourgeois settlement (0, 1) is, therefore

$$r_1 < g_1 v\theta/(1-g_1). \tag{83}$$

We get

Proposition 10. The inequality (83) is a necessary and sufficient condition for the evolutionary stability of the pure Bourgeois pair of strategies $(\hat{x}, \hat{y}) = (0, 1)$. By symmetry it is also a necessary and sufficient condition for the ESS property of the Desperado solution (1, 0).

Recall that $g_1 = \int_0^1 \phi(1-u)\,\mathrm{d}F(u)$ is the chance that an individual in its weakest possible condition $x = 1$ will win a contest with a random opponent, thus $0 \leqslant g_1 \leqslant 1/2$. The condition (83) for the pure Bourgeois ESS (0, 1), given private information to the opponent, is not surprisingly stronger than the condition (24) for such an ESS in the case of no private information. This, in turn, is stronger than the condition (64) for the existence of a mixed, non-Bourgeois ESS (or of the non-existence of the pure aggressive ESS). The three conditions coincide if $g_1 = 1/2$, which is the case if, and only if, the private information bears no consequence for the outcome of actual fights.

The condition (83) is never satisfied in the other extreme case $g_1 = 0$ in which the result of an actual private state of one contestant (indeed in this ca
intruder in a state close to 0 has no reason not t
hawk).

By straightforward calculations one can r
verify that

$$\frac{\partial^2 T_1(x,1;\hat{x},1)}{\partial x^2} < 0$$

for any value of $\hat{x}$. This means that if the reve
(83) holds but r_1 is sufficiently close to $g_1 v\theta/(1$
(i.e. if $\partial T_1(x, 1; 0, 1)/\partial x$ is below zero) then a v
exists, $\tilde{x}$ as close as we wish to 0 (depending
choice of r_1) such that

$$\frac{\partial T_1(x,1;0,1)}{\partial x} > 0 \quad \text{for} \quad x > \tilde{x}$$

$$\frac{\partial T_1(x,1;0,1)}{\partial x} < 0 \quad \text{for} \quad x < \tilde{x}$$

But, since sign $\partial T_1(x, 1; \hat{x}, 1)/\partial x)$ is indepe
on $\hat{x}$, $\hat{x} = \tilde{x}$ is the best answer to the ov
population strategy $\hat{y} = 1$. On the other hand,
arguments of continuity, for $\tilde{x}$ close enough
$\partial T_1(\tilde{x}, y; 1, \tilde{x}, 1)/\partial y$ is still negative, for all $0 \leqslant$
and we get

Proposition 11. If $g_1 v\theta/(1-g_1) < r_1 <$
$(1-g_1)+\delta$ for a value $\delta > 0$ sufficiently
then in addition to the symmetric ESS (
there is an ESS $(\tilde{x}, 1)$ where $0 < \tilde{x} < 1$ ($\tilde{x}$
close to 0).

This ESS represents a situation in which the
always defends its property while the intruder (
to yield most of the time) tends to fight under t
situation of extremely favourable conditions.

We refer to such an ESS as a quasi-Bourgeoi

Out of symmetry, in such a situation, there
also the quasi-Desperado ESS $(1, \tilde{x})$.

What remains to be considered is the p
existence of asymmetric ESS $(\hat{x}, \hat{y})$ and ($\hat{x} >$
addition to (x^*, x^*), in general intermediate
of parameters

$$g_1 v\theta/(1-g_1) < r_1 < (1-v-2g_1)\theta(2g_1)$$

We refer to an ESS $(\hat{x}, \hat{y})$, $(\hat{x} > \hat{y})$, if it exis
Weak-Bourgeois-ESS. It corresponds to a sit
commonly observed in nature, which the Ma
Smith-Parker-Grafen model failed to predict,
a situation in which both owner and intrud
occasionally play hawk, but it is the intruder
does it less often.

Out of continuity arguments we may specul
such an ESS exists at least for a partial ra

7. Conclusions

The models suggested in this work attempt to analyse the situation of an owner-intruder conflict as suggested by Maynard-Smith & Parker (1976) when, as suggested by Grafen (1987), each of the two opponents takes into consideration its chance of finding another property and the expected time it is supposed to hold either this specific property or any other one, if obtained. As mentioned by Grafen, both the chance of getting hold of a new property and the expected time one is supposed to hold a property once obtained, depend not only on the specific, local strategy chosen by the two opponents at the time of the conflict, but also on the strategy each of them intends to choose in the future when in the other role, and on the strategy $(\hat{x}, \hat{y})$ played by other individuals in the population. In addition, these two critical values of the population game depend on given ecological factors such as the availability λ of properties (either empty or occupied), on the chance v that a given property is empty, on the intensities ρ_1 and ρ_2 of natural death events among individuals (with and without property) and on the expected damage inflicted on a loser of a fight.

Given these parameters, the expected future time of ownership T_1 of an individual now without property and that, T_2, of a present-time owner, have been calculated as functions of the individual strategy (x, y), determining its action in either of the two roles, and of the population strategy. Under the assumptions that both owner and intruder each seeks to maximize its own expected future ownership time, the population game has been analysed and, despite its nonlinear structure, it has been shown that like in the simpler, linear model studied by Maynard-Smith & Price, all ESSs of the model are pure. When $\rho_1\lambda^{-1}$ is sufficiently large then the only ESS is (1, 1), that is total aggression. If it is below some critical level then the only ESSs are either (1, 0), (0, 1), or both. In the symmetric case, studied by Maynard-Smith & Parker, the critical condition is $\rho_1 = \lambda\theta v$.

If ρ_1 falls below this value, there are always two other ESSs, the Bourgeois ESS (0, 1) and the Desperado ESS (1, 0).

The situation is different if, for the same model, we assume that each individual has some information about its personal aptitude at the time of the conflict. In this case an individual choice of strategy, even if it appears to be random while observed by its opponent or by any outside observer, is rather determined by its own private information.

We have restricted our analysis, in this model, to intruder is outcome and payment irrelevant. It has been shown that, in this case, for any choice of parameters, a symmetric, non-Bourgeois ESS exists, in which any information about ownership is irrelevant to the behaviour of the opponents. Under a condition strictly stronger than the one required by the previous model, this symmetric ESS is (1, 1), that is to always play hawk. The two conditions only coincide if the private information of the opponent is irrelevant to the outcome of an actual fight, if it occurs. If ρ_1 is smaller than a critical value, determined by the ESS condition of (1, 1) a mixed non-Bourgeois ESS (x^*, x^*), $0 < x^* < 1$, exists. Yet it is shown that, in this case, this ESS may not be the only one allowed by the model. Other non-symmetric pairs of ESS $(\tilde{x}, \tilde{y})$ and $(\tilde{y}, \tilde{x})$ can also be maintained in which $\tilde{x} < \tilde{y}$. The ESS $(\tilde{x}, \tilde{y})$, in this case, is thus interpreted as a Weak Bourgeois ESS in which the owner more often tends to play hawk.

Moreover, when ρ_1 falls below a second critical value, lower than the one determined by the condition $\rho_1 < \lambda\theta v$, required in the previous model, the pure Bourgeois pair of strategies (0, 1) [but also (1, 0)] is a strict local ESS. The condition for this is strictly stronger than $\rho_1 < \lambda\theta v$ except for the limit case in which the private information is irrelevant to the outcome of an actual fight, if it takes place.

REFERENCES

ESHEL I. (1982). *Evolutionary and continuous stability. J. Theor. Biol.* **108,** 99–111.

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 contests: Anim. Behav.* **29,** 193–205.

HAMMERSTEIN, P. & RICHERT S. E. (1988). *Payoffs and strategies in territorial contests: Ess analyses of two ecotypes of the spider Agelenopsis Aperta: Evol. Ecol.* **2,** 115–138.

HARSANYI J. (1973). *Games with randomly disturbed payoffs: A new rational approach for mixed strategy equilibrium points. Int. J. Game Theory,* **2,** 1–23.

MAYNARD-SMITH, J. (1974). *The theory of games and the evolution of animal conflicts. J. Theor. Biol.* **47,** 209–221.

MAYNARD-SMITH J. & PRICE, G. R. (1973). *The logic of animal conflicts. Nature, Lond,* **246,** 15–18.

MAYNARD-SMITH, J. & PARKER, J (1976). *The logic of asymmetric contests. Anim. Behav.* **25,** 1–9.

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

APPENDIX

In this paper we followed, in a quantitative way, the argument of Grafen (1987) that the population game suggested by Maynard-Smith & Parker cannot must depend, in turn, on the very population strategy. More specifically it has been maintained by Grafen that, once the Bourgeois Principle is accepted by the population, the value of the intruder's life must be regarded less valuable than that of the owner, in sense that its expected future ownership time (say, EFOT) must be smaller.

In the terminology of this article:

$$T_1(0, 1; 0, 1) < T_2(0, 1; 0, 1) \qquad \text{(A.1)}$$

As one expects, this is, indeed, true.

Another statement of Grafen, which also sounds true, is that the acceptance of the Bourgeois Principle, although advantageous for the owners in the population, is obviously disadvantageous for the potential intruders as a group so it is not clear why they should accept it to start with (even though it is, indeed, to the advantage of both owners and intruders to keep to it, once it has been accepted as a rule in the population).

In the terminology of the article:

$$T_2(1, 0; 1, 0) < T_2(0, 1; 0, 1) \qquad \text{(A.2)}$$

$$T_1(1, 0; 1, 0) > T_1(0, 1; 0, 1). \qquad \text{(A.3)}$$

A surprising result, mentioned to us by Yoram Hamo, is that only the first of these two formulas is true. Employing equalities (5) and (11–14) from this
paper, and assuming a saturated environmen
easily gets the equality:

$$T_1(1, 0; 1, 0) = T_1(0, 1; 0, 1)$$

This means that, at least in terms of EFO
potential intruder is impartial to the Bou
equilibrium and the paradoxical one. It seems q
counterintuitive result if one keeps in mind the c
of the potential intruder to ever become an
before its natural death. Obviously this cha
lower at the Bourgeois equilibrium than a
paradoxical one. Yet, becoming an owner, the
is, indeed, larger at the Bourgeois equilibrium.
calculation indicates that from the point of vi
the potential intruder, these two factors e
compensate for each other. (It is shown, mor
that in the case of unsaturated environmen
reverse of (A.3) holds. This corresponds to a sit
in which the population is ever increasing and
EFOT of the owner, in case of the Bou
equilibrium, even overcompensates for the
chance of a potential intruder to ever beco
owner).

An intuitive argument for equality (A.3)′ is
by Hamo in a different article (1995). He en
this equality to show why is it likely that at
rational players, either owners or potential intr
will converge in choosing the Bourgeois st
which is the only ESS to which no player s
opposes.