attrition hypothesis, because the new occupant should have judged itself increasingly likely to win after it had spent more time on the territory. Krebs' (1982) data show that this assumption is true.

The main body of Getty's (1989) text addresses shortcomings of the war of attrition model to analyse the neighbour–stranger effect. He points out that the model requires a 'sealed bid' to be made and adhered to prior to each contest (or each successive round), so that information acquired during the contest cannot be used to alter the bid. It seems very likely that individuals do gain information during territorial contests and use it to adjust their tactics, and we agree with Getty that a more explicit discussion of the war of attrition model's assumptions is warranted. The question is, how much will information change the model's predictions? We do not know the answer. Parker (1984) points out that because of the information aspect, the war of attrition is far less suitable for analysing contests than it is for games against the field. We feel, however, that the analysis of territorial contests requires, in a general way, one contestant to evaluate the territory in relation to how others evaluate it, and to 'bid' accordingly. The war of attrition is our current metaphor for this process.

The main point of our paper about the neighbour–stranger effect (see also a related paper by Giraldeau & Ydenberg, 1987, on the 'centre–edge' effect) was to point out that when interactions between individuals for territories are being analysed a game theoretical approach is appropriate. A functional analysis of the centre–edge and neighbour–stranger effects had not previously been attempted, and we feel that the war of attrition models provide a consistent explanation for many of the empirical findings. We do agree with Getty's assertion that the simple war of attrition is probably an incomplete explanation, and may indeed ignore some of the most intricate and complex aspects of the whole phenomenon. The next step should not be to choose which of the available models is 'correct' (since all are abstractions, none can be, strictly speaking, correct), but rather to pursue theoretical and experimental work along several lines, in search of more insights. We feel especially that more experimental work explicitly aimed at testing game theoretical hypotheses is required, as is a game theoretical framework for treating contests in which information is exchanged. As Maynard Smith (1982) states, the latter is an important and difficult challenge, and our papers aimed to take a first step by taking well-described phenomena and applying game theoretical models.

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Are Dear Enemies in a War of Attrition?

Ydenberg et al. (1988) proposed that an asymmetric war of attrition model (Parker & Rubenstein 1981; Maynard Smith 1982; Parker 1984)' provides a consistent explanation' (page 346) for the dear-enemy phenomenon (Fisher 1954; Getty 1987). In this game players attempt to assess each other's fighting ability and motivation, and then they 'bid' a certain amount of time or cost. The bid should be drawn at random (i.e. unpredictably) from one of two distributions which correspond to the roles of winner (the high-bid distribution) or loser (the low-bid distribution). The player with the highest benefit-to-cost rate ratio should play the role of winner by drawing from the high-bid distribution. The highest bid wins. Unfortunately, the terminology can be confusing, or even misleading. If the bid distributions overlap, then occasionally the highest bid may be drawn from the low-bid distribution, so that the contestant playing the role of loser actually wins. Parker (1984) provides a summary.

The game is interesting only if players cannot assess each other's benefit-to-cost-rate ratios perfectly and as a consequence they occasionally make mistakes in adopting roles. The crux of the paper by Ydenberg et al. (1988) is that 'more aggression will be observed in contests in which role mistakes are more likely' and that 'role mistakes are more likely in neighbour–stranger contests than in neighbour–neighbour contests' (page 345). The usefulness of role mistakes in explaining territorial disputes depends on the appropriateness of the asymmetric war of attrition model. The model has some severely limiting assumptions that are not made clear in the presentation.

Ydenberg et al. (1988) imply that 'all the essential assumptions of the war of attrition would seem to be met' if 'contestants are able to regulate their investment in a contest continuously' and 'the costs of a contest increase with time spent in the contest' (page 343). Unfortunately, there is another assumption that can easily be lost behind the potentially ambiguous term 'continuously'. Contestants in a war of attrition draw their bids from continuous distributions before a contest begins, but they cannot alter them continuously during a contest. The players may assess each other before a fight, but they then must make sealed bids that cannot be altered once the fight begins. This means that a player that makes a role mistake is committed to play out the entire bid. The player cannot assess its progress during a fight and alter its bid by fleeing or escalating. This set of assumptions is appropriate when the contest involves displays of persistence that convey no information about ability or motivation, and that do not involve damage or anything that could affect the playing out of the bids (Maynard Smith 1982).

Ydenberg et al. (1988) point out that increased role mistakes would result in more aggression by two means: (1) directly by increasing the frequency of contests where both players play the winner role (bid from the high bid distribution), and (2) indirectly by altering the bid distributions (cf. Parker 1984). They do not consider that increased mistakes per se should also increase the frequency with which both players draw bids from the loser (low) distribution. More frequent double-low bids, as well as double-high bids should increase the variance in intensity, as well as the mean intensity. Recall that the duration or cost of a contest is set by the lowest bid. If, for instance, bid distributions are exponential (cf. Parker 1984), then the most frequent lowest bid should be approximately zero, even in the absence of role mistakes. Mistakes increase the frequency of zero-bid contests. I am not sure what this means in territorial disputes. Do the neighbour and stranger both abandon the territory? Although Ydenberg et al. (1988) state that' we need only assume that role mistakes are more likely' (page 345), I suspect that they are considering only one particular kind of mistake, that of a stranger inappropriately adopting the role of winner, and not the mistake of a neighbour inappropriately adopting the role of loser.

The ability to make continuous adjustments during a fight (in contrast to the ability to make bids before the fight that are not constrained to be discrete values) opens up much wider strategic possibilities (Parker 1984). Parker & Rubenstein (1981) attempted to deal with this by breaking each contest into a series of short rounds, each of which is a mini war of attrition with sealed bids. Contestants can use the outcome of each round to inform the bid for the next round. Their analysis is both constrained and complex, but they concluded that it becomes difficult to determine whether animals persist through a contest because of cost considerations or 'to obtain better information' (Parker & Rubenstein 1981, page 235).

In his discussion of Parker's work with dung flies, Maynard Smith (1982) concluded that a reasonable fit with the war of attrition model is probably dependent on the fact that contests are not iterated pairwise and thus information transfer is less likely to influence behaviour (page 35). In Parker's (1985) discussion of Maynard Smith's (1982) war of attrition model of territorial boundaries, he pointed out that 'a criticism would be that an ESS analysis ought to take into account the fact that territorial disputes are typically repeated contests' (page 55). A war of attrition model (in normal form, cf. Luce & Raiffa 1958) does not provide the best framework for analysing information exchange in repeated contests. Parker (1984) suggested that new models of games in extensive form (game trees, cf. Luce & Raiffa 1958) are required for these problems and that they will eventually replace the simpler war of attrition model.

If fighting is not constrained to involve a series of sealed bids, then there is a simple alternative to the role mistake hypothesis proposed by Ydenberg et al. We could call this the 'fighting to learn' hypothesis. Familiar neighbours fight very little because they have little to learn. They already know there is little to be gained from fighting each other again. Spatial economic considerations result in a boundary where the benefit–cost ratios reverse. Some fighting and learning are required to establish the boundary because displays are unreliable indicators of motivation (Maynard Smith 1982). Conditions may change, so some low level of probing may be ongoing. If conditions do change, neighbours will engage in escalated renegotiations (Ewald 1985). Strangers fight more because they have to learn if there is anything to be gained from fighting a particular opponent, not because they mistakenly play the role of winner and therefore irrevocably commit themselves to a big fight before the fight begins. Fighting to learn (probing) is like sampling resources in an unknown, but a posteriori, poor habitat patch. It can be misleading to interpret either as a mistake, because it may be a priori the best thing to do (Getty et al. 1987).

In addition to these learning and mistakes hypotheses, there are other possible reasons why territory residents discriminate between neighbours and non-neighbours (Getty 1987). For instance, neighbours may be in a position to bargain in ways that are not available to non-neighbours, and non-neighbours may pose a greater threat to usurp the entire territory, rather than just pilfer some food. The only alternative mentioned by Ydenberg et al. (1988) is reciprocal altruism between neighbours. They dismiss this alternative with the comment 'we do not need to invoke reciprocal altruism' (page 343), presumably because they are satisfied that' the asymmetric war of attrition model provides a consistent explanation' (page 346). If a war of attrition model does indeed provide the best explanation of the dear-enemy phenomenon (as opposed to another consistent explanation), then it is in spite of some rather restrictive assumptions and the existence of several alternatives.

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Aposematism and Bioluminescence

A recent paper by Grober (1988) examines the intriguing idea that the bioluminescent flashes of brittle-stars function as aposematic signals to deter crab predators. We would like to criticize Grober's paper on two counts. First, although Grober concludes that brittle-star bioluminescence is aposematic, we do not believe that his experiments demonstrate this. Second, we find his discussion of the evolutionary issues misleading.

Grober claims that his study demonstrates that bioluminescent signals can function as an aposematic predator deterrent (page 493), so it is important to understand why he is wrong. The theory of aposematism was developed by Poulton (1890) after an original discussion between Darwin and Wallace (Wallace 1867) over the use, by insect larvae, of bright coloration to advertise unpalatability. Both then, and more recently (e.g. Cott 1940; Edmunds 1974; Gittleman & Harvey 1980; Roper & Redston 1987; Guilford 1988), the theory has clearly been regarded as an adaptive explanation of the incidence of conspicuousness in unprofitable prey. Adaptation implies selective advantage, so the critical prediction of aposematism is that the relevant cue (here luminescence) be a more effective warning signal than its alternative (no luminescence) and it is generally accepted that, except where avoidance reactions are innate, this must constitute a special ability to enhance the acquisition and maintenance of learnt aversions (Gittleman & Harvey 1980; Harvey & Paxton 1981;