EVOLUTIONARY ANALYSIS OF THREAT AND FIGHTING IN THE AMERICAN COOT (*Fulica americana*)

by

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ABSTRACT

Breeding American Coots (*Fulica americana*) aggressively defend territories in which they nest and obtain the food necessary to raise their young. Interactions between neighbouring territory owners are frequent, time consuming, and may escalate to severe physical fights. Most interactions however are resolved through the use of a wide range of threat displays. Such an array of threat displays was traditionally interpreted as communication between opponents, resulting in a mutually beneficial resolution. Game theoretical work has questioned this perspective, because theoretically it seems that a cooperative exchange of information could not be evolutionarily stable. It has been suggested that a variety of threat displays can be stable when their risk (probability a given display will provoke a dangerous physical response) and effectiveness (probability that the display will win an interaction) are correlated.

I examined territorial interactions between neighbouring American Coots during two breeding seasons (1991-92) near Creston, BC, and found no correlation between the risk and effectiveness of the behaviours used during aggressive interactions. The source of the failure of game theory to explain these results may lie

in some assumptions made by the theories that are violated in the coot system. However, there was information exchanged in the sense that the choice of behaviour influenced both the opponents reply, and subsequent behaviours by the original actor.

The second part of my thesis studied information exchange in a dynamic model. The model considered a game between two players competing over a non-divisible prize. During the contest players signal their perceived relative fighting ability to each other, and base their estimates upon signals received. The model showed that neither complete honesty, nor complete ambiguity could be stable. Rather, it seemed that a judicious balance of bluff and honesty was best.

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CHAPTER 1

INTRODUCTION: EVOLUTIONARY ANALYSES OF THREAT AND AGGRESSION

Historical Context

Aggression is one of the most studied aspects of animal behaviour, and it's history is a thumbnail sketch of the history of the study of animal behaviour. Classical ethology described agonistic behaviour in terms of releaser signals (Tinbergen, 1953), motivational drives (Lorenz, 1966), and internal states (Cullen, 1966). Under this paradigm a ritualized threat display is an external manifestation of the true internal state of the animal, allowing direct comparison of desire to win, and thus settling a conflict without dangerously violent acts (Huxley, 1966).

Current individual-selectionist accounts of animal contests have relied heavily on the theory of games and the notion of an evolutionarily stable strategy, ESS (review in Maynard Smith, 1982). The first theoretical analyses of animal fights used two games: the War of Attrition (Maynard Smith & Parker, 1976; Bishop & Cannings, 1978), and the Hawk-Dove game (Maynard Smith & Price, 1973; Maynard Smith & Parker, 1976; Maynard Smith 1982). The Hawk-Dove game demonstrates that the resolution of agonistic encounters through the use of conventional, or ritualized, displays can be evolutionarily stable. While this explanation of ritualized aggression is widely accepted, graded signals, or multiple threat display types, remain "something of a puzzle" (Dawkins & Krebs, 1978).

The problem is revealed by the application of the second game theory paradigm, that of the war of attrition (Maynard Smith & Price, 1973; Maynard Smith & Parker, 1976; Bishop & Cannings, 1978; Maynard Smith, 1982), to the matter of escalation. The spirit of the war of attrition is this; bids are made, and the cost of contesting is directly related to the (eventual loser's) bid size. The contest is won by the contestant making the higher bid, while both contestants pay according to the lower bid. A bid can be almost any costly act, energetic cost of displaying (Rand & Rand, 1976), chase duration, (Marden & Waage, 1990), or response intensity (Price <u>et al.</u>, 1990). The positive relation between bid and cost (the bid-cost function) keeps the game stable, and it is therefore obvious that the game would be unstable if any communication of bids occurs, since contestants can then change their actual costs based on their opponent's bids. Any attempt to circumvent the cost of a bid makes the whole process unstable, since bids become meaningless once costs are allowed to be manipulated after the bid has been made.

In the case of multiple display types the bid has been assumed to be related to the intensity of the threat display (Ydenberg et al., 1988). Species with multiple threat displays would therefore appear to communicate their cost intentions when the war of attrition clearly shows it to be evolutionarily unstable (Parker, 1984). This thinking prompted Caryl (1979) to re-analyze data from four published works claiming to demonstrate such communication (Stokes, 1962a&b; Dunham, 1966; Andersson, 1976), and to conclude that while individuals did reliably signal intentions to retreat, threats, in the sense of a reliable predictor of attack, were not made; some behaviours consistently preceded an escape, but none reliably presaged an actual attack (Caryl, 1979). Counter to this result, an increasing amount of experimental evidence (Bossema & Burgler, 1980; Nelson, 1984; Enquist et al., 1985; Popp, 1987b&c; Senar, 1990; Waas, 1991a; but see also; Paton & Caryl, 1986; Paton, 1986) continues to indicate that animals communicate intentions during contests.

Enquist et al. (1985) proposed a mechanism that would allow stable communication of intentions in threat displays. Stability can be maintained by preserving the bid-cost function. Enquist et al. (1985) defined the "effectiveness" of a threat display as the probability that when used, the sender will win a fight over a contested resource, and he defined the cost as the probability that the use of the display leads to potentially dangerous fighting. If the cost and effectiveness of different threat displays are correlated, then they can all co-exist in a repertoire. Subsequent studies of multiple threat displays have confirmed such a preservation of the bid-cost function between behaviours (Enquist et al., 1985; Popp, 1987b&c; Senar, 1990; Waas, 1991a).

Agonistic behaviours may communicate more than just short term intentions. Communication of resource holding potential (RHP) (Parker, 1974), the physical ability to win an all-out fight, is the classic alternative to the communication of intentions. Game theorists have speculated that communication about RHP could be stable (Maynard Smith, 1979) and empirical work has established this communication (Hazlett, 1968; Davies & Halliday, 1978; Clutton-Brock & Albon, 1979; Beeching, 1992). Enquist and Leimar have developed a formal model, the sequential assessment game (Enquist & Leimar, 1983; Leimar & Enquist, 1984). The sequential assessment game models a system in which an actor "probes" the opponent with displays, interpreting "samples" returned according to insurance mathematics models to determine the opponents RHP.

The general goal of this thesis was to use the above paradigms to investigate the role of threat, understood as co-operative information exchange, in animal contests. My specific objectives were to:

1) Analyze the behaviour of a territorial animal, with respect to information exchange during agonistic contests. Specifically, I wanted to test whether the risk and effectiveness of the threat displays of the American Coot (Fulica americana) were correlated.

2) Model a system in which information about fighting ability was exchanged, to explore the possibility that honest information exchange may be a stable strategy.

In Chapter 2, I analyze territorial interactions between American Coots with respect to the information content of the behaviours used during interactions. I examine contests observed in the field for a correlation between the cost and benefits of different displays in various agonistic contexts.

In Chapter 3, I investigate theoretically whether contestants can benefit by signalling their perception of their fighting ability relative to their opponent.

In Chapter 4, I present a synthesis and summary of the issues in agonistic communication.

CHAPTER 2

THE RISK AND EFFECTIVENESS OF THREAT BEHAVIOUR IN THE AMERICAN COOT (*Fulica americana*)

INTRODUCTION

Ethological studies prior to the application of game theory assumed that threat displays were accurate manifestations of internal state (Cullen, 1966), and that the intentions of the actor were strictly driven by these states. Thus displays could be compared and the most aggressive individual could claim the prize without risking injury (Tinbergen, 1959). Agonistic confrontations involving multiple displays were seen as fluctuations of internal state and conflicting drives within each animal (Cullen, 1966).

Empirically, the ethological approach to the analysis of communication was to demonstrate correlation between consecutive actions by one animal, and between an actor's behaviour and it's opponents reply. Such communication is about intentions, since it can be used to predict subsequent behaviours. Correlations between consecutive acts by the same individual have been found found (eg. Stokes, 1962a&b; Dunham, 1966; Andersson, 1976), though reanalysis shows that these results are questionable (Caryl, 1979). Subsequent efforts in the same vein have demonstrated that correlative links between past and future behaviours exist in some cases (Bossema & Burgler, 1980; Nelson, 1984; Senar, 1990; Waas, 1991a), and not in others (Paton & Caryl, 1986).

For a repertoire of threat displays to be evolutionarily stable requires that displays have costs and benefits that are highly correlated: the more effective the threat, the higher the cost should it fail to work (Hinde, 1981; Enquist et al., 1985). The benefit, or effectiveness (probability that a threat works and wins a confrontation) of a more intensified display should be matched by escalation of the cost (the risk of physical injury; Enquist et al., 1985). This prediction has been met in several species (Enquist et al., 1985; Popp, 1987a&b; Waas, 1991b; Senar et al., 1992).

American Coots (Fulica americana) are well known for their vicious attacks upon intruders in their territory (Gullion, 1953). The reproductive success of coots is limited by food availability for the chicks (Lyon, 1992). This means that territory area is a vital resource base. These territories are typically on the order of 20-30m in diameter. Coots spend almost all the daylight hours, and much of the night, swimming about their territories. Neighbouring coots often meet, frequently swimming across their entire territory to join in a confrontation. Neighbouring pairs engage in numerous, prolonged, interactions along relatively stable territory boundaries (Gullion, 1953; Sutherland, 1987). The large number of aggressive displays

(Gullion, 1952) used by coots make them an appropriate species for the study of fighting behaviour.

In this chapter I examine the territorial and aggressive behaviour of a population of coots for evidence of reliable communication of intentions, and for correlation of risk and effectiveness of displays.

METHODS

Study site and organism

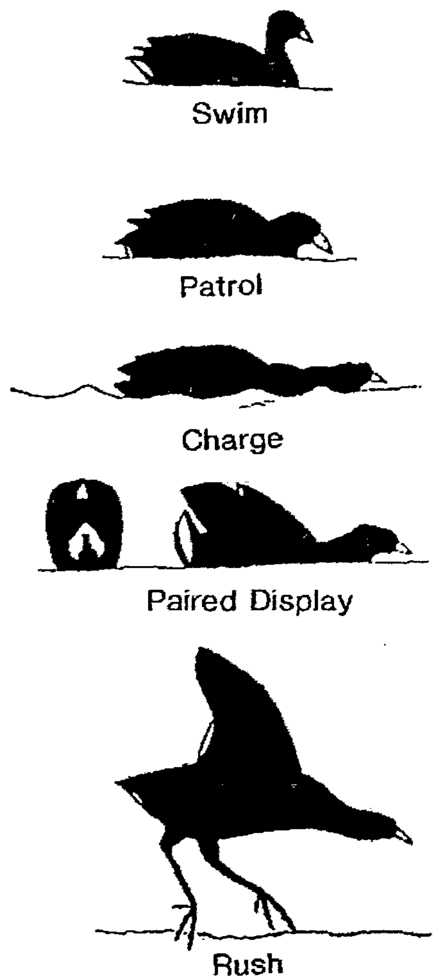
All field work was conducted in Leach Lake, at the Creston Valley Wildlife Management Area near Creston, B.C. (49°05'N, 116°35'W). Leach Lake is divided into four distinct ponds. Ponds 2,3, and 4 were included in the 1991 season, all work during 1992 was conducted in Pond 2. Pond 4 is characterized by dense Common Cattail (Typha latifolia) stands and proved to be highly unsuited for coot watching and nest monitoring. In contrast the dominant emergent plant in Ponds 2 & 3 was Hardstem Bulrush (Scirpus acutus). In Pond 3 this emergent growth was very sparse, providing very little cover for nests. Both nests and eggs were visible from large distances, suggesting that this was marginal habitat, and blinds had to be placed far from the nests.

Pond 2 seemed ideal habitat for both coot and coot researcher. Bulrush clumps were dense, but sufficiently far apart to allow both ample cover for nests and good visibility for coot watching. Generally one or two clumps were contained in each territory. Nests were easily found and monitored during nest searches, conducted every three or four days. Usually new nests were anticipated, as pairs new to the area were fairly obvious, and their movements easily followed. Territory boundaries were noted for purposes of anticipating conflicts and detecting any gross changes in ownership of areas.

Coot displays

Coots use four distinct styles of locomotion; Swim, Charge, Patrol, and Rush (see Fig 2.1). When Swimming the bird is in normal posture, the head is held up, and the under tail coverts are inconspicuous (Gullion, 1952). A Coot spends almost all it's time in the Swim posture, this is the normal, or base-line posture, it is more a lack of display than a display. The Charge posture is quite striking, the head and neck are stretched out along the water surface, the bird swims quickly leaving a prominent wake (Gullion, 1952). The Patrol posture is more subtle, the head is held low to the water and the back of the wings are slightly raised, higher than the head. The Patrol posture occasionally gives the impression of being intermediate between the Charge and Paired Display postures (see below). Gullion's (1952) description of the Patrol display with reference to neck ruff erection and tail feather depression was too fine for positive identification during interactions, and the posture aspects cited above were used as the distinguishing attributes. When Rushing (Splattering according to Gullion, 1952) the bird flaps it's wings as it runs

Figure 2.1 Selected agonistic behaviours of the American Coot



Splatter, resembles Rush except that the wings are held against the body, the head is held low, and the bird remains stationary. From Gullion (1952).

across the water surface. A Rush is apparently the fastest way a coot can get from one place to another.

In addition to locomotory behaviours, coots use a wide array of other behaviours in aggressive contexts. The Paired Display is the most striking of all coot displays, the head is held low and the wings fully arched over the back and extended to the sides. The white under tail coverts are flared and prominent. Opponents usually perform this display simultaneously, close together (hence 'paired' display), while spinning slowly around on the spot. Splattering (Churning according to Gullion, 1952) has a definite auditory component, the bird raises it's body out of the water by rapidly stamping the water surface, the head is lowered and the wings are held folded in against the body. Two separate 'ruffling' displays were recorded, Ruffle-Wing Extension, in which the bird shook it's body while stretching it's wings, and Ruffle-Humple, in which the body and legs cleared the water as the body shook. Dabble, Feed, Preen, Stand On Mound, and Dive are all fairly self explanatory behaviours that were recorded in aggressive contexts.

Other behaviours were recorded only rarely. Hide Behind Bulrushes, Foot Attack While Airborne and Dive In Pursuit were neither stereotypical behaviours, nor composed of existing stereotypical behaviours, and so were described as accurately as possible at the time of recording. Two behaviours that were recorded, the Head-bob and the Body-up, merit specific mention here. Head-bobs were seen only in specific individuals, before and between foot-fight bouts, as well as during apparently tense face-to-face confrontations when foot-fighting seemed imminent. Head-bobbing was performed while the bird was sitting still in the water, and resembled the head motions associated with swimming. This behaviour was difficult to score, as it could easily be interpreted as the initiation of turning. This behaviour was not uniformly recorded between observers, and is not analyzed further, though it merits further study as a high level threat display.

Similarly the Body-up was recorded only late in the 1992 season, though it had been seen often before. Foot-fighting coots roll back on their tails and sit in an upright posture to grab and rake the opponent with their claws. This posture is what is referred to as Body-up. The Body-up posture was seen only during foot-fights until late in the 1992 season, when one bird in particular attempted foot-fighting only to have it's opponent back out of range. This sequence happened several times, producing the impression that the Body-up posture was a very high-intensity threat, and not just an inherent part of foot-fighting. Since the body-up was only seen outside of footfighting late in the study, it's analysis as a threat would be largely post-hoc, and is not analyzed separately here.

Data collection

Coots were observed from a blind or parked vehicle using a spotting scope (Bushnell Spacemaster II 15-45 X 70), binoculars (Bushnell ensign 7 X 50, Tasco 8 X 30) or unassisted. Behaviour sequences were recorded using a lap top computer (TRS-80) programmed as an event recorder, a tape recorder (Realistic CTR-85, or Micro 12) or written directly onto paper. Tape recording was the preferred method. Data were recorded using sequence sampling (Altmann 1974). Individuals were monitored ad-lib, and if it appeared that the focal animal was not likely to get into a confrontation in the near future, another individual was observed. Fights already in progress were not recorded (since important preliminary stages had obviously already been missed) unless physical contact between individuals occurred, in which case the behaviours immediately preceding contact were recorded. The resulting behavioural sequences, those leading to physical contact but lacking the initial stages leading to physical contact, are referred to as "Snips". Locations of fights in progress were noted for the purposes of estimating territory boundaries.

Recorded observations consisted of the sequence of behaviours that constituted an aggressive interaction. An action in a sequence was recorded whenever either contestant changed from one behaviour to another, or changed from facing Towards it's opponent to facing Away or vice versa. These Towards and Away orientations were recorded for all locomotory behaviours, whether or not there was any appreciable change in distance between opponents. Parallel facing was occasionally recorded in the field, but for the purposes of data analysis, parallel facing was converted to Towards, or Away before analysis. A parallel facing bird was considered to be facing away from it's opponent if it was the first orientation recorded for the animal in the sequence, otherwise parallel facing was considered to be the opposite of the previously recorded facing.

A bird was judged to have won an interaction if it displaced it's opponent, gained ground by ending the interaction inside it's opponent's territory, or caused the opponent to retreat in any appreciable way. Table 2.1 provides an explanation of a sample sequence from the data set.

Table 2.1 Sample behavioural sequence

Behavioural Sequence First Year (1991) #69b.

1CT; 2PA-WA; 1WA; 2PA; 1WT-A-PT-WA; 2PA-DAB; 1PT-ST-DAB-SA; 1(P2N29F)WINS,2(P2N7SF)LOSES #F69b

	Contestant 1		Contestant 2	
	Posture	Facing	Posture	Facing
contest begins	Charge	Towards		
	"	"	Patrol	Away
	"	"	Paired	"
	Paired	Away	"	"
	"	"	Patrol	"
	Paired	Towards	"	"
	"	Away	"	"
	Patrol	Towards	"	"
	Paired	Away	"	"
	"	"	Patrol	Away
	"	"	Dabble	"
	Patrol	Towards	"	"
	Swim	"	"	"
	Dabble	"	"	"
	Swim	Away	"	"
contest ends	Wins		Loses	
Bird ID	Pond 2; Nest 29 female		Pond 2; Nest 7south female	

Measuring risk and effectiveness

Risk is defined as the probability that a given display leads to physical fighting. Immediate risk is the probability that a given display is immediately followed by physical contact, while total risk is the probability that a given display leads to physical fighting before the end of the confrontation.

The effectiveness of a display is defined as the probability of winning an interaction after using a particular display. Ideally, effectiveness can also be measured as immediate or total. Unlike previous studies, conducted at feeders, or in other situations where losers immediately left the site (eg Bossema & Burgler, 1980; Enquist et al 1985; Popp, 1987a,b&c; Senar, 1990; Senar et al, 1992), no measure of immediate effectiveness can be made here, since no single instant can be identified as the point where an interaction is conclusively decided. Total effectiveness, whether a contest was eventually won or lost after a given behaviour, was the only measure of effectiveness possible.

It is hypothesized that this measure of display effectiveness will correlate with the risk associated with using that display.

RESULTS

A total of 867 behavioural sequences were scored, 294 in 1991, 573 in 1992. These sequences were further classified by contestant types (territory owner or non-territorial birds, adult or subadult), whether or not the observer could decide who had won, and whether the interaction involved more than two individuals. Obviously the data were not all of equal usefulness, and different data were included in the working data set for tests of different hypotheses.

Predicting behaviour

Two analyses for independence between behaviours were used in order to determine whether any measurable information exchange was occurring between contestants. The first analysis considered every case in which an actor's behaviour was replied to, and the reactor's response was then replied to by the actor. This sequence is described as A, B, and C behaviours. These trios of behaviours were drawn from the entire N=4782 pool of behavioural sequences (with the exception of the Snips data points, and those sequences dropped from the contingency tree data set on account of beginnings which could not be described as escalation. These could not be described in an A, B, C, trio, since the appropriate B, opponent, behaviour didn't exist to separate the initiator's displays. In those cases in which several escalating initial behaviours were performed before a response occurred, all but the behaviour preceding the reply were dropped. Tests of independence showed that all effects and interactions were highly significant (Table 2.2). This means that reply behaviours (B to A, and C to B) are sensitive to the behaviours they are replies to (A and B respectively), and that a link therefore exists between a behaviour and the previous behaviour by the same individual (A and C).

The second analysis considered the effect of winner (initiator wins, non-initiator wins or a tie) and actor (non-initiator replies to initiator or vice versa) on behaviour-reply pairs. Action-reaction pairs ($\underline{N}$ = 3832) were drawn from those entire behaviour sequences in which two territory owners competed. These pairs were then classified by Winner, Role, versus the First behaviour and the Reply behaviour, as detailed in Table 2.3. Log-linear model analysis of the tables shows highly significant effects for each effect and interaction, except for the role by winner interaction, first behaviour by reply behaviour by winner interaction, and the four way interaction (Table 2.4). This means that the overall behaviour-reply pattern was significantly different when winners replied to losers, compared to when losers replied to

Table 2.2 Reply contingency between a behaviour, the opponent's reply, and the actor's following behaviour

	PARTIAL ASSOCIATION		
EFFECT	D.F.	CHISQ	PROB
C.	10	3072.34	0.0000
B.	10	3023.41	0.0000
A.	10	3350.05	0.0000
CB.	140	1228.69	0.0000
CA.	183	2072.65	0.0000
BA.	152	947.00	0.0000
CBA.	756	1251.82	0.0000

Where A, B, and C are the first second and third behaviours in a trio. Behaviours A and C are performed by one individual, behaviour B by it's opponent.

Table 2.3 Contingent behaviour / reply pairs by role (initiator or non-initiator is replying) and winner (initiator wins or non-initiator wins)

Table 2.3A Initiator Wins - Replies to Initiator

	SA	ST	PA	PT	CA	CT	WA	WT	RA	RT	SP	FG
SA	45	7	6	0	1	1	3	2	2	0	0	0
ST	84	11	7	2	5	2	8	2	5	1	0	0
PA	11	2	4	1	2	0	2	0	1	0	0	0
PT	7	4	7	0	2	2	3	0	10	0	0	0
CA	6	3	0	0	2	1	7	0	0	1	0	0
CT	156	24	23	7	33	24	65	14	25	3	0	0
WA	62	12	20	12	5	24	89	40	1	7	1	0
WT	16	4	8	5	2	3	61	34	8	3	0	0
RA	1	0	0	0	0	0	3	1	1	4	0	0
RT	40	1	1	0	7	5	46	11	119	11	0	2
SP	0	0	0	0	0	0	0	0	1	0	0	0
FG	0	1	0	0	0	0	1	1	4	0	0	

Rows are behaviours by initiator, and winner, columns are reply behaviours of non-initiator and loser.

SA is Swim Away, ST is Swim Towards, PA is Patrol Away, PT is Patrol Towards, CA is Charge Away, CT is Charge Towards, WA is Paired Away, WT is Paired Towards, RA is Rush Away, RT is Rush Towards, SP is Splatter, and FG is Fight.

Table 2.3B Initiator Wins - Initiator replies to Opponent

	SA	ST	PA	PT	CA	CT	WA	WT	RA	RT	SP	FG
SA	84	68	13	8	6	62	39	7	1	43	0	1
ST	10	9	1	4	1	16	13	3	0	4	0	0
PA	11	7	7	6	2	11	14	6	0	2	0	0
PT	3	1	1	0	0	5	9	4	1	1	0	0
CA	9	4	3	1	4	15	11	3	0	7	0	0
CT	2	1	0	3	3	12	31	7	0	2	0	0
WA	26	9	5	2	8	31	91	63	1	28	0	1
WT	5	1	3	1	0	5	45	28	2	10	0	2
RA	16	14	3	1	1	23	42	8	2	44	1	3
RT	1	1	0	0	1	3	9	5	3	2	0	4
SP	0	0	0	0	0	0	1	0	0	0	0	0
FG	0	1	0	0	0	0	6	0	0	0	0	

Rows are behaviours by non-initiator and loser, columns are reply behaviours of initiator, and winner.

SA is Swim Away, ST is Swim Towards, PA is Patrol Away, PT is Patrol Towards, CA is Charge Away, CT is Charge Towards, WA is Paired Away, WT is Paired Towards, RA is Rush Away, RT is Rush Towards, SP is Splatter, and FG is Fight.

Table 2.3C Initiator Loses - replies to Initiator

	SA	ST	PA	PT	CA	CT	WA	WT	RA	RT	SP	FG
SA	11	15	5	1	1	11	3	3	0	6	0	0
ST	5	5	2	2	1	5	2	0	0	2	0	0
PA	3	1	0	3	0	0	2	1	0	0	0	0
PT	2	2	0	2	0	0	1	0	0	0	0	0
CA	2	3	0	1	0	0	0	0	0	1	0	0
CT	8	5	2	3	2	7	7	0	0	1	0	0
WA	6	6	1	2	1	5	17	9	0	2	1	0
WT	1	0	0	1	0	2	3	3	0	2	0	0
RA	3	3	0	0	0	2	3	2	0	6	0	0
RT	2	0	0	0	0	2	3	4	1	2	0	1
SP	0	0	0	0	0	0	0	0	0	0	0	0
FG	0	0	0	0	0	0	1	0	0	0	0	

Rows are behaviours by initiator and loser, columns are reply behaviours of non-initiator, and winner.

SA is Swim Away, ST is Swim Towards, PA is Patrol Away, PT is Patrol Towards, CA is Charge Away, CT is Charge Towards, WA is Paired Away, WT is Paired Towards, RA is Rush Away, RT is Rush Towards, SP is Splatter, and FG is Fight.

Table 2.3D Initiator Loses - Initiator replies to Opponent

	SA	ST	PA	PT	CA	CT	WA	WT	RA	RT	SP	FG
SA	17	6	2	1	2	4	4	2	0	0	0	0
ST	20	1	4	2	3	2	5	0	0	0	0	0
PA	5	1	0	0	0	1	2	0	0	0	0	0
PT	4	1	3	2	0	1	2	1	0	0	0	0
CA	1	1	0	0	0	1	0	0	0	0	0	0
CT	9	2	1	0	3	2	8	1	3	2	0	0
WA	9	1	2	1	0	4	14	3	1	2	0	1
WT	3	0	1	0	0	1	8	3	2	3	0	1
RA	0	0	0	0	0	0	0	0	0	0	0	1
RT	3	1	0	0	0	0	5	2	11	4	0	0
SP	0	0	0	0	0	0	1	0	0	0	0	0
FG	0	0	0	0	0	0	1	1	1	0	0	

Rows are behaviours by non-initiator, and winner, columns are reply behaviours of initiator and loser.

SA is Swim Away, ST is Swim Towards, PA is Patrol Away, PT is Patrol Towards, CA is Charge Away, CT is Charge Towards, WA is Paired Away, WT is Paired Towards, RA is Rush Away, RT is Rush Towards, SP is Splatter, and FG is Fight.

Table 2.3E No winner - replies to Initiator

	SA	ST	PA	PT	CA	CT	WA	WT	RA	RT	SP	FG
SA	7	1	6	0	0	1	3	2	0	0	0	0
ST	5	4	2	0	0	3	4	2	0	0	0	1
PA	9	3	4	4	1	1	4	1	0	0	0	0
PT	1	0	4	1	1	0	3	0	0	0	0	0
CA	2	0	1	0	0	0	0	0	0	0	0	0
CT	22	7	12	4	5	13	17	6	0	0	0	0
WA	15	4	14	7	3	10	55	44	0	0	0	0
WT	6	1	1	2	4	5	28	26	0	2	0	1
RA	0	0	0	1	0	0	2	0	1	4	0	0
RT	2	2	2	3	1	5	20	6	8	3	0	1
SP	0	0	0	0	0	0	1	0	0	0	0	0
FG	0	0	0	0	0	0	0	0	1	0	0	

Rows are behaviours by initiator, columns are reply behaviours of non-initiator.

SA is Swim Away, ST is Swim Towards, PA is Patrol Away, PT is Patrol Towards, CA is Charge Away, CT is Charge Towards, WA is Paired Away, WT is Paired Towards, RA is Rush Away, RT is Rush Towards, SP is Splatter, and FG is Fight.

Table 2.3F No winner - Initiator replies to Opponent

	SA	ST	PA	PT	CA	CT	WA	WT	RA	RT	SP	FG
SA	11	7	4	1	3	9	6	1	0	0	0	1
ST	1	2	3	0	0	5	5	1	0	2	0	0
PA	7	2	12	1	1	3	8	2	0	3	0	0
PT	4	0	2	1	0	3	7	1	1	1	0	0
CA	1	1	1	2	0	1	5	3	0	1	0	0
CT	2	2	1	0	3	3	19	7	0	2	0	0
WA	11	2	9	6	0	8	56	31	1	9	1	3
WT	5	1	2	0	0	4	49	22	1	3	0	1
RA	1	1	0	0	0	0	2	1	1	3	0	0
RT	0	1	0	0	0	0	4	4	4	1	0	0
SP	0	0	0	0	0	0	0	0	0	0	0	0
FG	1	0	0	0	0	0	3	1	0	0	0	

Rows are behaviours by non-initiator, and winner, columns are reply behaviours of initiator and loser.

SA is Swim Away, ST is Swim Towards, PA is Patrol Away, PT is Patrol Towards, CA is Charge Away, CT is Charge Towards, WA is Paired Away, WT is Paired Towards, RA is Rush Away, RT is Rush Towards, SP is Splatter, and FG is Fight.

Table 2.4 Reply contingency as a function of initiation role and eventual winner

	PARTIAL ASSOCIATION		
EFFECT	D.F.	CHISQ	PROB
r.	11	3006.62	0.0000
f.	11	2735.74	0.0000
a.	1	10.66	0.0011
w.	2	1728.49	0.0000
rf.	271	1491.97	0.0000
ra.	11	211.40	0.0000
rw.	22	136.83	0.0000
fa.	11	563.44	0.0000
fw.	22	146.94	0.0000
aw.	2	0.46	0.7960
rfa.	102	164.34	0.0001
rfw.	202	222.86	0.1498
raw.	22	209.99	0.0000
faw.	23	246.77	0.0000
rfaw.	119	129.06	0.2491

Where r is reply, f is first behaviour, a is the actor (whether initiating bird, or non-initiating bird is the reactor), and w is winner (initiator wins, loses or ties).

winners, and that similarly significant differences existed in the pattern of replies to eventual losers and winners.

Risk

Ninety five instances of physical fighting were observed in 77 of the 876 behavioural sequences. Table 2.5 lists the frequency that given behaviours immediately preceded a physical attack. Separate tallies are presented for both the "Actor" (the individual who most recently changed behaviour) and "Non-Actor". Generally the Non-Actor performed a behaviour which provoked the Actor to attack. Thus a typical physical attack is initiated by the 'Non-Actor' performing a Rush Towards or Paired Away behaviour, then the 'Actor' performs a Rush Towards, and a foot-fight ensues. Also presented in Table 2.5 is the baseline count, N, of the number of occurrences of these behaviours in the complete data set, less those contained in the Snips subset (which were a biased subset, consisting exclusively of the prelude to physical contact). The actual immediate risk is presented as the frequency with which a behaviour immediately preceded a physical attack. It is presented in three forms, for Actor risk, Non-Actor risk, and the sum of Actor and Non-Actor, Summed Risk.

The result is that Splatter is the most risky

Table 2.5 Immediate risk of dangerous replies to aggressive behaviours, expressed as the proportion of times the behaviour preceded a physical attack.

Behaviour	Preceded Attack		N	Risk		
	Actor	Non-Actor		Actor	Non-Actor	Summed
Splatter	0	2	18	0	.1111	.1111
Rush Towards	48	27	744	.0645	.0363	.1008
Paired Towards	23	8	749	.0307	.0107	.0414
Rush Away	7	2	390	.0179	.0051	.0231
Paired Away	7	18	1660	.0042	.0108	.0151
Charge Towards	4	8	1072	.0037	.0075	.0112
Charge Away	0	2	201	0	.0100	.0100
Patrol Towards	0	1	158	0	.0063	.0063
Swim Away	3	2	1146	.0026	.0017	.0044
Dive	0	1	230	0	.0043	.0043
Swim Towards	1	0	579	.0017	0	.0017
Change* Partner	2	0	N.A.	-	-	-

For each Display is listed the number of times that it directly preceded a physical attack. N is the number of times the display in question appears in the whole data set. The Actor is the bird who changed behaviour most recently before physical contact, thus one behaviour was scored for each contestant per physical contact (exception see text).

* Change partner, the birds previous behaviour was physical fighting with a third bird.

behaviour overall (though this may be largely due to it's rarity), followed by Rush Towards, Paired Towards, and Rush Away.

<u>Display use: winners and losers</u>

The data in which two territory owners competed and produced a clear winner and loser were pooled to produce 439 contests. The number of contests in which the winners and losers performed any of the following behaviours: Swim, Patrol, Charge, Rush, Paired Display, Splatter, Ruffle-Humple, Ruffle-Wing Extend, Ruffle, Feed or Dive, and the Towards or Away facing of the first five displays, were scored. Differences between the degree to which winners and losers used these displays are presented in Table 2.6. Winners use the Swim Towards, Charge Towards, and Rush Towards behaviours significantly more, while losers were significantly more likely to Swim Away, Charge Away or Rush Away. Put more simply, losers retreated, winners advanced.

<u>Correlating the use and associated risk of behaviours</u>

Behaviours were ranked according to both risk and use by winners. Only behaviours which appeared in both Tables 2.5 and 2.6 were used. Rankings of use by winners were assigned in order of χ^2 values, (Table 2.6). χ^2 values were considered negative if the display was used more often by losers than winners.

Table 2.6 Association of display use with respect to eventual winner and loser

Behaviour	Used by Winner	Used by Loser	x^2	p	Rank Order
Swim Towards	142	82	21.63	<0.001	3
Swim Away	143	300	113.10	<0.001	10
Patrol Towards	30	29	0.02	N.S.	7
Patrol Away	51	61	1.02	N.S.	N.A.
Charge Towards	281	79	193.04	<0.001	1
Charge Away	26	47	6.13	<0.05	9
Rush Towards	205	50	134.47	<0.001	2
Rush Away	17	132	107.05	<0.001	11
Paired Towards	91	81	0.72	N.S.	6
Paired Away	212	181	1.38	N.S.	5
Splatter	4	4	0	N.S.	8
Ruffle Humple	28	19	1.82	N.S.	N.A.
Ruffle Wing Ext.	20	30	2.12	N.S.	N.A.
Feed	135	117	1.81	N.S.	N.A.
Dive	60	42	3.60	N.S.	4

The total number of sequences in this pool, ie highest possible score, was 439. Rank ordering of association of behaviours with winning was calculated only for those behaviours also listed in Table 2.2
Rank ordering is explained on page 32.

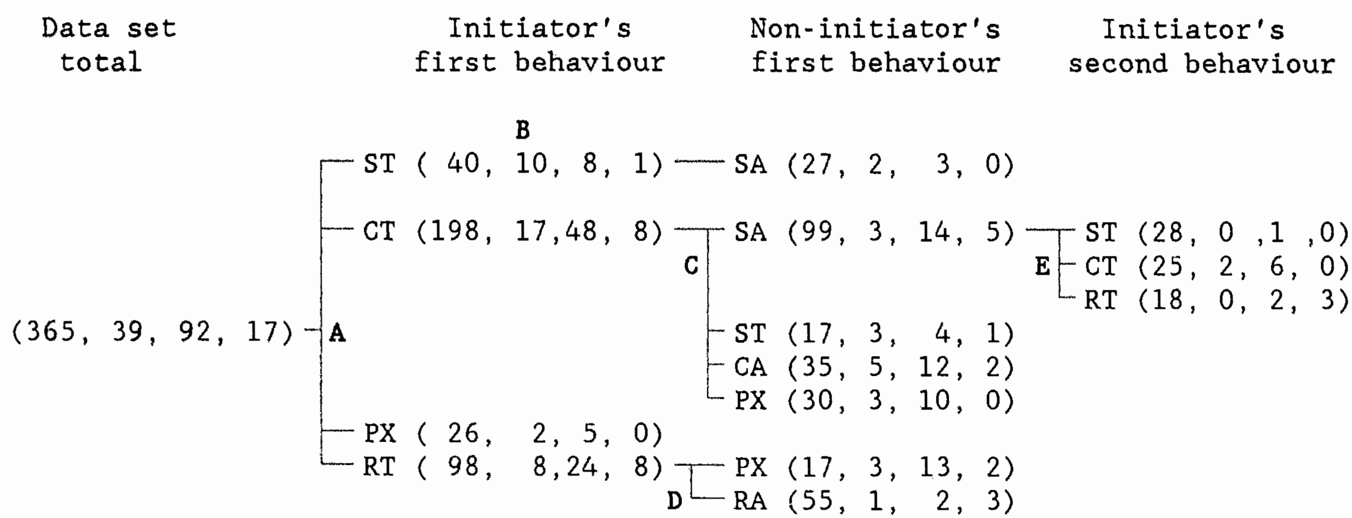
Three risk rankings were calculated using the Actor Risk/$\underline{N}$, Non-Actor Risk/$\underline{N}$, and Summed Risk/$\underline{N}$ measures (Table 2.5). Using Spearman rank order correlations I found no significant correlation between any of the three risk measures and their use by winners $\underline{r}_s$($\underline{N}$ =,7,10 & 11) = -0.036, 0.309 & -0.082, Actor, Non-actor & $\Sigma/\underline{N}$, respectively., all N.S.

Effectiveness and risk: the contingency tree

In order to calculate effectiveness accurately, behavioural decisions must be compared between sequences which are identical up to the display in question. The 485 behavioural sequences were grouped into a contingency tree (Fig 2.2). The sequences used were ones in which only two territory owners competed. Sequences in which the initiator changed behaviour in a manner that could not be described as escalation before the opponents first behaviour were not included. Instances where first behaviours of Swim or Patrol Towards were escalated to Charge, Paired Display, or Rush were kept, as were escalations from Charge to Paired, or Rush Towards.

Each contestant's change in behaviour, or continuance of a previous behaviour after an opponent's change in behaviour, was considered a branch point in the tree. Dive behaviours were scored as Swim Away, Feed & Dabble were ignored if performed in conjunction

Figure 2.2 The contingency tree



ST is Swim Towards, SA is Swim Away, CT is Charge Towards, CA is Charge Away, PX is Paired Display, RT is Rush Towards, RA is Rush Away.

The first number in the brackets is the number of sequences in which the initiator won, the second number is the number that the non-initiator won, the third number is the number of ties. Together the first three digits add to the number of behavioural sequences at that point. The fourth number is the number of sequences which contained physical fighting downstream from that point. Bold letters mark the branch, they are referred to in the text and Table 2.4. The initiator is choosing between behaviours at branch **A** and **E**, non-initiator is choosing at branches **C**, and **D**.

with Swim, Patrol, or Paired displays, but treated as a Swim display if following a display which could not be performed while feeding. The Paired Away and Paired Towards displays were combined into a common Paired category, and a final threshold for inclusion of a behaviour into the tree was set at $\underline{N} \geq 20$ at the behaviour point. The contingency tree left four branch points for 14 behaviours, A, C, D and E (Fig 2.2). A risk and effectiveness measure was then determined for each behaviour point.

Risk was defined as the probability that a sequence downstream from that point contained physical fighting. Effectiveness was defined as the probability that sequences downstream did resulted in a win or tie for the contestant currently choosing a behaviour. Cases in which no winner was scored were counted as a win for both contestants, considering the system under study this seemed reasonable.

G statistics (Williams' corrected) on branch points A, C, D and E (See Fig 2.2 and Table 2.7) showed no significant differences in risk between behavioural options at any of the branch points $G(3) = 2.688$, 1.638, 0.015, and 4.260, all $\underline{p} > 0.5$, at branch points A, C, D & E respectively. Note that no comparisons between behaviours can be made at branch point B, since there was only one reply to an initial Swim Towards

Table 2.7 Measures of risk and effectiveness of behaviours at points on the contingency tree

Behaviour	Branch	N	Effectiveness	Risk
Swim Towards	A	58	.8276	.0172
Charge Towards	A	263	.9354	.0304
Paired	A	33	.8485	0
Rush Towards	A	130	.8615	.0615
Swim Away	B	32	.1563	0
Swim Away	C	116	.9741	.0431
Swim Towards	C	24	.8750	.0417
Charge Away	C	52	.9038	.0384
Paired	C	43	.9333	0
Paired	D	33	.3721	.0465
Rush Away	D	58	.0862	.0517
Swim Towards	E	29	1	0
Charge Towards	E	33	.9394	0
Rush Towards	E	20	1	.2273

Behaviour points are listed according to the behaviour, and the branch point after which they occur (see Fig 2.2).

behaviour that was recorded ten times or more times (the threshold for analysis) in the dataset. Significant differences were found in the effectiveness of different options at branch points C and D G(3) = 17.370 and 11.778 respectively, both $\underline{p}<.005$, but not at branch points A and D G(3) = 6.567 and 1.793 respectively, both $\underline{p}>0.5$. This means that when replying to a Rush Towards (branch point D), the non-initiator is significantly more likely to win by using a Paired Display, than with a Rush Away. Similarly a non-initiator replying to a Charge Towards (branch point C) is significantly less like likely to win by Swimming Towards than if it had chosen to perform a different behaviour, such as Charge Away.

Pooling all fourteen branch points into a single plot produced a non-significant correlation between risk and effectiveness $\underline{r}_s(\underline{N}=14) = 0.234$, N.S. This means that, over the whole tree, all the different behaviours at each branch point showed no relationship between how effective they were in winning a contest, and how likely they were to eventually lead to physical fighting.

DISCUSSION

The sensitivity of subsequent behaviour to preceding acts demonstrates that in the coot system, information about intentions was being exchanged. Significant differences between use of displays by winners and losers were also found. However, these differences in use could not be correlated with the immediate risk of using these displays. Examined more closely, total effectiveness and total risk of behaviours were not found to be related. This non-significant result may be due to context specific or sequence sensitive, effects. Various behaviours may be used in contexts, such as inside the owner's territory, or outside, to which the analyses were not sensitive. Some behaviours may have different effects when used early, and late in an interaction, or before or after another behaviour, such as the Paired Display. While information is being exchanged, just what the value of this information is remains totally unclear.

The absence of a correlation between risk and effectiveness is also quite problematic, not so much for theoretical reasons, as much as for further analysis. In particular, the analysis of variation between individuals with respect to the tendency to escalate is frustrated by the inability of the dataset to provide an empirical ranking capable of serving as a measure of escalation.

Aggressiveness is defined as the tendency to escalate a fight, rather than the ability to win it (Rohwer, 1982; Studd & Robertson, 1985a; Maynard Smith & Harper, 1988). Barlow et al., (1986) found that individual cichlids showed persistent aggressiveness differences, and that these differences settled contests when both individuals were new to the area. These contests were typical of those found in the field. But, if contestants were allowed to establish ownership before encountering each other, then escalated, species atypical, fights ensued. These contests were decided by body size, which was not correlated with aggressiveness measures (Barlow et al., 1986). This latter sort of conflict is an RHP fight, the former more closely matches typical contests in nature.

Many aggressive interactions between animals are between individuals who have met before (van Rhijn, 1980), and may recognize each other. Under these conditions, the bid/cost function can be integrated over a longer period. In the case of the coots, one expects the RHP asymmetries between neighbours to be quite well known to both, and assuming RHP to be fairly constant, communication must then be about aggressiveness and intentions to escalate.

Watching coots interact gives the strong impression that a constant re-negotiation of territory boundaries is occurring. The paired display in particular seems to be used to end an interaction, with opponents performing the display to each other from either side of the territory boundary. Slight movements back and forth over the boundary strike the observer quite strongly as explicit haggling over small scale changes in the boundaries position (pers. obs., & assistant's pers. comm.). If an intruder performed a paired display inside the centre of a territory, the opponent would Rush Towards and physical fighting would be quite likely follow.

While the above description is highly subjective, it embodies much of the cooperative/conflict flavour of the dear enemy hypothesis (Fisher, 1954). Briefly, it is hypothesized that neighbours will cooperate in defensive coalitions to the extent that their past interactions have settled territorial conflicts, conflicts that would have to be repeated were a new neighbour to replace the known "dear enemy", (Getty, 1987). It is not known what the combined effect of dear enemy defensive coalitions, and accurate knowledge of the opponent's RHP, will be on communication. Without a formal model, it is not out of the question that these effects could maintain evolutionarily stable communication through displays, while the bid/cost function predications made for strangers competing over a non-divisible resource fail to be met.

CHAPTER 3

BAYESIAN BOXERS: ASSESSMENT AND INFORMATION EXCHANGE IN THREAT AND FIGHTING

INTRODUCTION

While early game theory suggested that communication of intentions was not evolutionarily stable, not all information exchange is necessarily communication of intent. There remains information about ability, for example visual assessment of body size (Enquist & Jakobsson, 1986; Enquist et. al., 1987), or status (e.g. Rohwer, 1977; Rohwer & Rohwer, 1978). Theoretical speculation was that unequally-matched contestants should communicate their RHP (Resource Holding Potential, Parker, 1974), or ability to win an all out fight (Maynard Smith, 1979). But a signal of RHP through some arbitrary display, would, intuitively, seem to be quite susceptible to 'bluffing' by competitively inferior cheaters.

Current theoretical work on communication of ability in agonistic encounters revolves around the sequential assessment game (Enquist & Leimar, 1983). Information in this game is modeled as an updating of estimated relative fighting ability (the difference between the opponent's RHPs), where this estimate is gained by sampling the opponent's fighting ability in a series of bouts. The actor prompts a reactor with a threat, and interprets the respondent's behaviour as a sample. This sample is combined with the current estimate, producing a new information state in the actor. The threatened individual supplies a response from a fixed function. No variability in the reliability of information produced by the threatened individual is modeled.

Here I develop a dynamic programming sequential assessment game. This model is an exercise in placing the stochastic element in the reactor. An actor makes a threat and a sample is returned from the reactor ("Fear" or "No Fear") according to some stochastic function. The precise function is the reactor's strategy, and is based on a Bayesian estimate of relative fighting abilities. The actor processes the information received using a Bayesian updating procedure which calculates exact assessments of the probability of each possible opponent RHP level. The only stochastic element in the exchange lies in what type of reply the reactor produces when threatened. The probability of returning a 'fear' sample is a function of the threatened individual's perception of the RHP asymmetry. This model allows a closer inspection of the issues of bluff and honesty in aggressive communication.

THE MODEL

Basic overview

This model describes competition over a non-divisible resource by two strangers. Each contestant knows it's own RHP (**RHP_e**)(e is for ego), but not it's opponent's (**RHP_o**)(o is for opponent) or what samples it has returned to it's opponent. Each contestant also knows the population distribution of RHPs (**Y**). In each turn both players must choose one of the three behavioural options: Quit, Threaten or Fight. Estimates of opponent RHP are updated based on the response to Threats. Possible outcomes for each contestant are Win, Lose without sustaining an injury, and Lose with an injury. Losing with injury returns no fitness, uninjured losers collect a residual fitness, and winners receive the residual fitness plus the prize value.

In choosing to Quit a contestant ensures that it will lose without injury, while the opponent wins. By choosing Fight the actor (ego) attempts to take the prize, and the probabilities of success and injury are determined as a function of the difference between ego and opponent's RHP values. Both Quit and Fight are endpoints, in that the contest is resolved in favour of one of the contestants when one of these behaviours is selected.

Threat returns a response of 'fear' or 'no-fear' from the opponent. The probability of a 'fear' sample being returned is based on the opponent's assessment of the differences in fighting ability between the contestants. The assessment is crucial to the strategy because the estimated chances of winning a fight, and the probability of injury, are derived from that difference. With each Threat, the actor improves it's assessment of the opponent's RHP.

Stochastic Dynamic Programming is used to derive the set of optimal behaviours under all possible combinations of state. Forward iteration is then used to calculate the expected fitness of each RHP and Role combination.

Two versions of the model are presented. In the first (simple) model, all contestants use the same function for determining the probability of responding to a threat with fear. The second version, the variable strategy model, considers the case when different players use different functions for determining how to respond to threats.

<u>Model dynamics</u>

The program proceeds through successive time intervals **t**=1,2,3...T, and terminates (if neither contestant has yet chosen Quit or Fight) at T=10. Contestants alternate choices in each time interval, with player A acting (being 'ego') first, and player B second.

Contestants' states are described by two state variables; number of times the opponent responded to a threat with fear, **n**, and fighting ability, $\mathbf{RHP_e}$. Since Threat is the only non-endpoint behavioural option, one state variable tracking the number of fear samples returned is sufficient, since the number of "no fear" samples must equal **t-n**. The second state variable, $\mathbf{RHP_e}$, is more of a parameter than a variable, in that contestants are assigned an $\mathbf{RHP_e}$ value, and cannot change during a contest. But all values of $\mathbf{RHP_e}$ must be calculated in parallel, and hence are programmed as a state variable.

Contestants know their own fighting ability, $\mathbf{RHP_e}$, the number of fear samples returned, **n**, the population distribution of fighting abilities, **Y**, and the time, **t**. The contestants do not know their opponent's fighting ability, $\mathbf{RHP_o}$, nor do they know the number of fear samples collected by their opponent, $\mathbf{n_o}$. Through calculations developed below, accurate probabilistic estimation of these opponent states variables is possible.

<u>Decisions</u>

Quit returns a payoff equal to residual fitness, $\mathbf{V_r}$, (lose without injury) to the quitter, (equation 1).

$$Payoff(Q) = V_r \qquad (1)$$

(Note that a residual fitness plus prize value, $\mathbf{V_k}$, minus the cost of a threat, $\mathbf{C_d}$, times the number of threats made, $\mathbf{t}$, is returned to the winning opponent if ego quits. This eventuality pays to ego only if it threatens an opponent whose next behaviour is to quit. See the Threat option below.)

The payoff to a Fight behaviour is 1 minus the probability of getting injured, ω (a function of the asymmetry, **a**, between $\mathbf{RHP_e}$, and $\mathbf{RHP_o}$) multiplied by $\mathbf{V_r}$, plus the probability of winning, π (also a function of **a**), multiplied by $\mathbf{V_k}$, minus the number of threats made (which equals **t**, the number of turns taken, minus one) times the cost of a threat, $\mathbf{C_d}$, (equation 2).

$$payoff(F) = [(1-\omega)\,V_r + \pi\,V_k] - (t-1)\,C_d \qquad (2)$$

Note that ω and π, are functions of $(\mathbf{RHP_e}-\mathbf{RHP_o})$. This means that in order to calculate the expected payoff of fighting, a contestant must have an estimate of $\mathbf{RHP_o}$.

The estimate is made by threatening the opponent and observing the response. The mechanism behind this estimation is presented below (see Estimating opponent state).

With increasing numbers of Threats made, the accuracy of the estimates of opponent RHP increases. Since threat is a non-end point, the opponent will then make a reply behaviour. To evaluate the Threat payoff, it is necessary to know what the opponent's next behaviour ($\mathbf{B_o}$) will be. Obviously, the choice of current behaviour is sensitive to the probability that the opponent will reply with a Quit, Threat or Fight behaviour. Finding the opponent's reply is simply a matter of checking the opponent's optimal behaviour set for the opponent state (the combination of opponent's **RHP**, **t**, and **n**) under consideration. The actor must do this for each possible **RHP**, and **n**, to calculate an independent probability of each combination.

If the opponent's next move is to Quit then the payoff to threatening the opponent is the factor of the probability that the opponent is of that state, and the value of winning ($\mathbf{V_r}$ plus $\mathbf{V_k}$), less $\mathbf{t} \times \mathbf{C_d}$, the direct cost of performing a threat display ($\mathbf{C_d} \ll \mathbf{V_r}$ & $\mathbf{V_k}$), (equation 3).

$$payoff(T) = V_k + V_r - t(C_d) \quad |\mathrm{B}_o = 'Q' \qquad \textbf{(3)}$$

If the opponent's next behaviour is Fight, then the value is as if the actor had chosen to fight (see above), less one extra $\mathbf{C_d}$ for the extra threat, factored by the probability that the opponent is of the state in question, (equation 4).

$$\begin{aligned} payoff(T) = & (1-\omega(a))\pi(a)(V_r + V_k - t(C_d)) \\ & + (1-\pi(a))V_r - C_d \quad |\mathrm{B}_o = 'F' \end{aligned} \qquad \textbf{(4)}$$

If the opponent's next behaviour is Threaten, then the payoff (factored by probability that it is the state of the opponent) is Ψ_a times the fitness at t+1, n+1, at that same $\mathbf{RHP}_{ego}$ plus 1-Ψ_a times the fitness at state t+1, n, $\mathbf{RHP}_e$, all less $\mathbf{C}_d$, (equation 5).

$$\begin{aligned} payoff(T) = &\Psi_e(a)\,\Phi_e(RHP_e, n+1, t+1, T) \\ &+(1-\Phi_e)\,(RHP_e, n, t+1, T)\,|\mathbf{B}_o='T' \end{aligned} \qquad (5)$$

<u>The fear, no-fear mechanism</u>

Ψ_a is the probability that the opponent responds with fear to a threat by the ego. For the simple model runs, Ψ_a was calculated using equation 6.

$$\Psi_a = \frac{RHP_e - RHP_o + RHP_{max}}{10} \qquad (6)$$

Table 3.1 and Fig 3.1 show this function,(Ξ_1 in Fig 3.1).

In the variable strategy model, individuals played one of five different Ψ_a functions, as shown in figure 3.1. All Ψ_a functions were linear and varied only in slope. An additional state variable, Ξ_e, was used to track the Ψ_a, function an individual played, each Ξ_e value corresponding to a Ψ_a function. Functions with a low slope are less reliable indicators of **RHP**. Thus Strategy 1 is the most informative, and Strategy 5 the least informative. The Ψ function used in the simple model was the most reliable of the five functions used

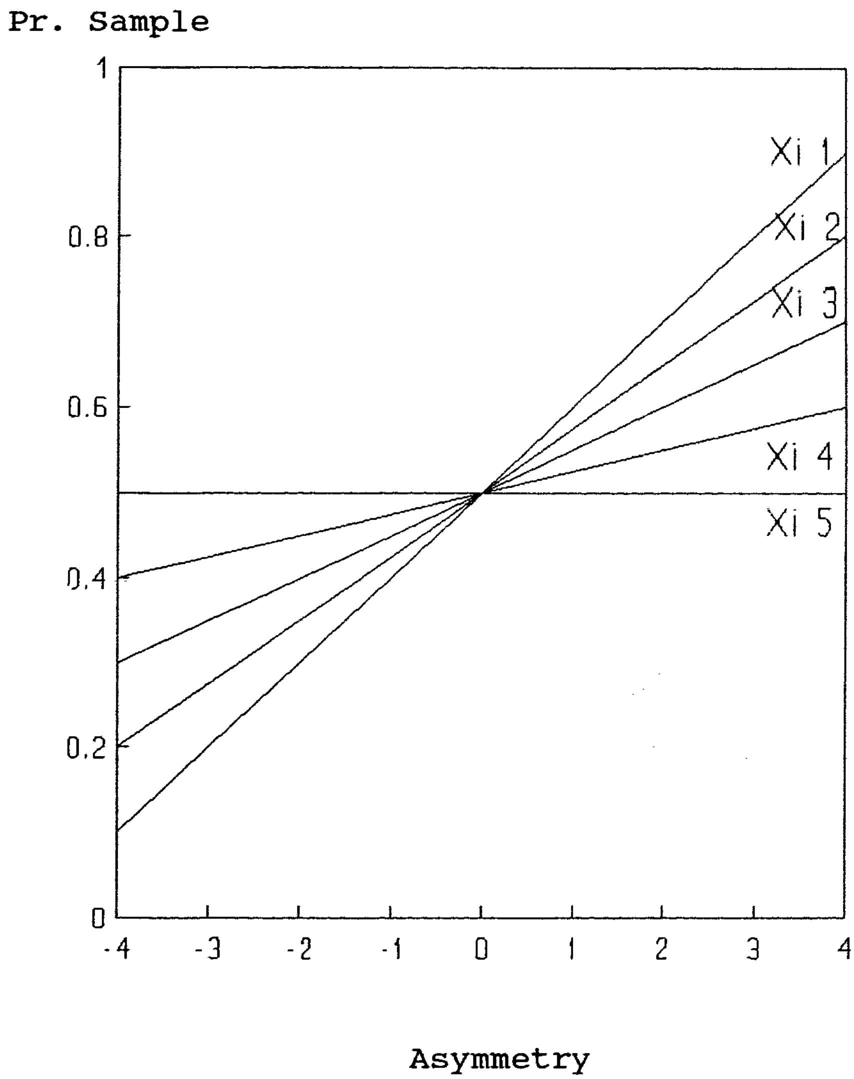
Table 3.1. Parameter values used

RHP	Υ
1	0.1
2	0.2
3	0.4
4	0.2
5	0.1

a	π_a	ω_a	Ψ_a
-4	0.1	0.3	0.1
-3	0.2	0.25	0.2
-2	0.3	0.2	0.3
-1	0.4	0.2	0.4
0	0.5	0.15	0.5
1	0.6	0.1	0.6
2	0.7	0.05	0.7
3	0.8	0.02	0.8
4	0.9	0.01	0.9

Υ is the population distribution of RHPs
a is RHP asymmetry, (RHPe-RHPo)
π_a is the probability of winning a fight
ω_a is the probability of injury in a fight
Ψ_a is the probability of returning a fear sample, the function here equals Ξ_1 in the variable strategy model.

Figure 3.1. Strategy sets, Xi functions.



Where Asymmetry is RHP_e-RHP_o, Pr. Sample is the probability that the opponent will return a 'no fear' sample, and Xi_1 to Xi_5 are Ξ_1 to Ξ_5.

Note that the simple model used $\Xi 1$ exclusively.

in the variable strategy model.

Estimating opponent state

As we have seen, estimation of the payoffs to the Fight and Threat options requires that the actor have an estimate of opponent RHP and n. While a contestant does not know it's opponent's RHP, it is able to calculate, and update on each turn, an exact probability distribution of $\mathbf{RHP_o}$, given **t**, **n**, and Ψ (the probability of returning a sample as a function of **a**). The heart of the model is calculation of probability distributions for the opponent's possible states. The payoffs for each opponent state must be weighted by the estimated probability that the opponent is actually of that state. The equations to solve for these probabilities are derived below.

The binomial process

$$Pr(n|t,n) = \binom{t}{n} \Psi^{n} (1-\Psi)^{t-n} \tag{7}$$

is a binomial distribution with mean Ψ, and **n** is the number of instances (fear samples) occurring in **t** time intervals. Using Bayes's theorem,

$$Pr(X_i|Y) = \frac{Pr(X_i)\ Pr(Y|X_i)}{Pr(Y)} \tag{8}$$

where

$$Pr(X_i) = Y_i \tag{9}$$

$$Pr(Y) = \Sigma_i Pr(n, t, \Psi_i') \, Pr(\Psi_i = \Psi_i') \tag{10}$$

$$Pr(y|X_i) = Pr(n, t, \Psi_i') \tag{11}$$

thus

$$Pr(\Psi_i'|n, t) = \frac{Y_i Pr(n, t, \Psi_i')}{\Sigma_i Pr(n, t, \Psi_i') \, Pr(\Psi' = \Psi_i')} \tag{12}$$

<u>The dynamic programming equation</u>

Formally, the DPE is

$$\Phi_e(RHP_e, n, t, T) = \max \begin{cases} V_r & |\mathbf{B}_e = 'Q' \\ \sum_{RHP_o=1}^{RHP_i} Pr_{RHP_o} \sum_{n_o=0}^{\{t|A,\ t+1|B\}} Pr_{n_o} \, VB_o & |\mathbf{B}_e = 'T' \\ \sum_{RHP_o=1}^{RHP_i} Pr_{RHP_o} \, VF_o & |\mathbf{B}_e = 'F' \end{cases} \tag{13}$$

where

$$Pr_{RHP_o} = \frac{\mathbf{Y}_{RHP_o} \binom{t}{n} \Psi^n_{RHP_o} \, (1 - \Psi_{RHP_o})^{t-n}}{\sum_{RHP_i=1}^{RHP_{max}} \mathbf{Y}_i \binom{t}{n} \Psi^n_{RHP_i} \, (1 - \Psi_{RHP_i})^{t-n}} \tag{14}$$

Note that the binomial t choose n can be cancelled out, yielding (this was not done in computational version),

$$Pr_{RHP_o} = \frac{\Upsilon_{RHP_o} \Psi^{n}_{RHP_o} \ (1-\Psi_{RHP_o})^{t-n}}{\sum_{RHP_i=1}^{RHP_{max}} \Upsilon_i \Psi^{n}_{RHP_i} \ (1-\Psi_{RHP_i})^{t-n}} \qquad \textbf{(15)}$$

$$Pr_{n_o} = \binom{t}{n_o} \Psi^{n_o}_{RHP_{e-o}} (1-\Psi_{RHP_{e-o}})^{t-n_o} \qquad \textbf{(16)}$$

$$VB_o = \begin{cases} V_k + V_r - t(C_d) \ |\mathbf{B}_o(n_o, t) = 'Q' \\ (1-\omega_a)\pi_a(V_r + V_k - t(C_d)) + (1-\pi_a) V_r - C_d \quad |\mathbf{B}_o(n_o, t) = 'F' \\ \Psi_{(e,a)} \Phi_e (RHP_e, n+1, t+1, T) + (1-\Phi_e)(RHP_e, n, t+1, T) \quad |\mathbf{B}_o(n_o, t) = 'T' \end{cases} \qquad \textbf{(17)}$$

$$VF_o = (1-\omega_a)((\pi_a V_k - (t-1) C_d) + V_r) \qquad \textbf{(18)}$$

A & B role, or the actor currently optimizing
e & o are Ego, and Opponent
$\mathbf{a}$=RHP_e-RHP_o
$\mathbf{V_r}$= Residual fitness, ie expected fitness in future years.
$\mathbf{V_k}$= The increment in fitness for winning the prize.

C_d= The immediate cost of making a threat.
$B_o(n_o,t)$=opponent's next behaviour
γ=Pop. Dist. and Prior dist. of RHPs
π_a=Pr(win)
ω_a=Pr(damage)
Ψ_a=Pr(fear)

V_r and V_k were set to 0.333, and 0.667, respectively, maximum fitness is then 1.0. Other parameter functions are shown in Table 3.1.

Formally, the DPE does not change when applied in the variable strategy model, but the Ψ function changes from a linear function of RHP_{e-o} to a plane function of $\Xi_e \times RHP_{e-o}$. Computationally, the program is changed by looping through the original program inside nested Ξ_B and Ξ_A loops.

Use of different Ψ functions for different contestants did not require that actors have knowledge of the opponent's strategy. Estimates of the opponent's response were performed by interpreting samples according to the ego's own Ψ strategy. Possibly problematic mismatch between stochastic reality (the actual state of the opponent), and the ego's expected relation to that reality were avoided by using the opponent's Ψ function during the forward iterations. Thus the backward iterations use the ego's strategy to generate the optimal behaviour matrix, and the forwards iterations use the opponent's. The decision to use the ego's Ψ function to interpret the opponent's actions was made to simplify computation.

Initialization

The DPE cannot be implemented directly at T because it requires a set of existing values to work backwards from. These initial values are the payoffs at T. The rules change slightly at the end of the game, player B cannot threaten on the very last move of the game, for instance, and player A's last move must be made with the knowledge that B will not play 'threat' next. The modified DPE for the initialization phase is

$$\Phi_B(RHP_B, n, T, T) = \max \begin{cases} V_I \quad |\mathbf{B}_B = 'Q' \\ \sum_{RHP_A=1}^{RHP_I} Pr_{RHP_A} VF_A |\mathbf{B}_B = 'F' \end{cases} \tag{19}$$

for player B, and

$$\Phi_A(RHP_A, n, T, T) = \max \begin{cases} V_I |\mathbf{B}_A = 'Q' \\ \sum_{RHP_B=1}^{RHP_I} Pr_{RHP_B} \sum_{n_B=0}^{T} Pr_{n_B} \; VB_B \; |\mathbf{B}_A = 'T' \\ \sum_{RHP_B=1}^{RHP_I} Pr_{RHP_B} VF_B |\mathbf{B}_A = 'F' \end{cases} \tag{20}$$

where,

$$VB_B=\begin{cases} V_k+V_r-T(C_d)\,|\mathrm{B}_B(n_B,T)='Q' \\ (1-\omega_a)\pi_a(V_r+V_k-T(C_d))+(1-\pi_a)V_r-C_d|\mathbf{B}_B(n_B,T)='F' \end{cases} \qquad \textbf{(12)}$$

for player A. All other terms are as defined above for the regular DPE, $VF_{A\&B}$ are the same as the general VF_o, where t is now equal to T.

Calculating fitness

Fitness was calculated by working forward through the solution sets generated in the backward iterations. For each state, the probability of each possible outcome was calculated, and probability densities were passed on to t+1 states. As endpoints were reached, the payoffs were weighted by the probability densities of the states in which they were reached. Mirroring the rationale used in the backward iterations, only one forward iteration per solution set was needed, since this was not a Monte Carlo simulation, but a parallel cumulative calculation of all possible states and outcomes. This results in expected fitnesses for each contestant and RHP_e combination, not in an average calculated from multiple instances.

RESULTS

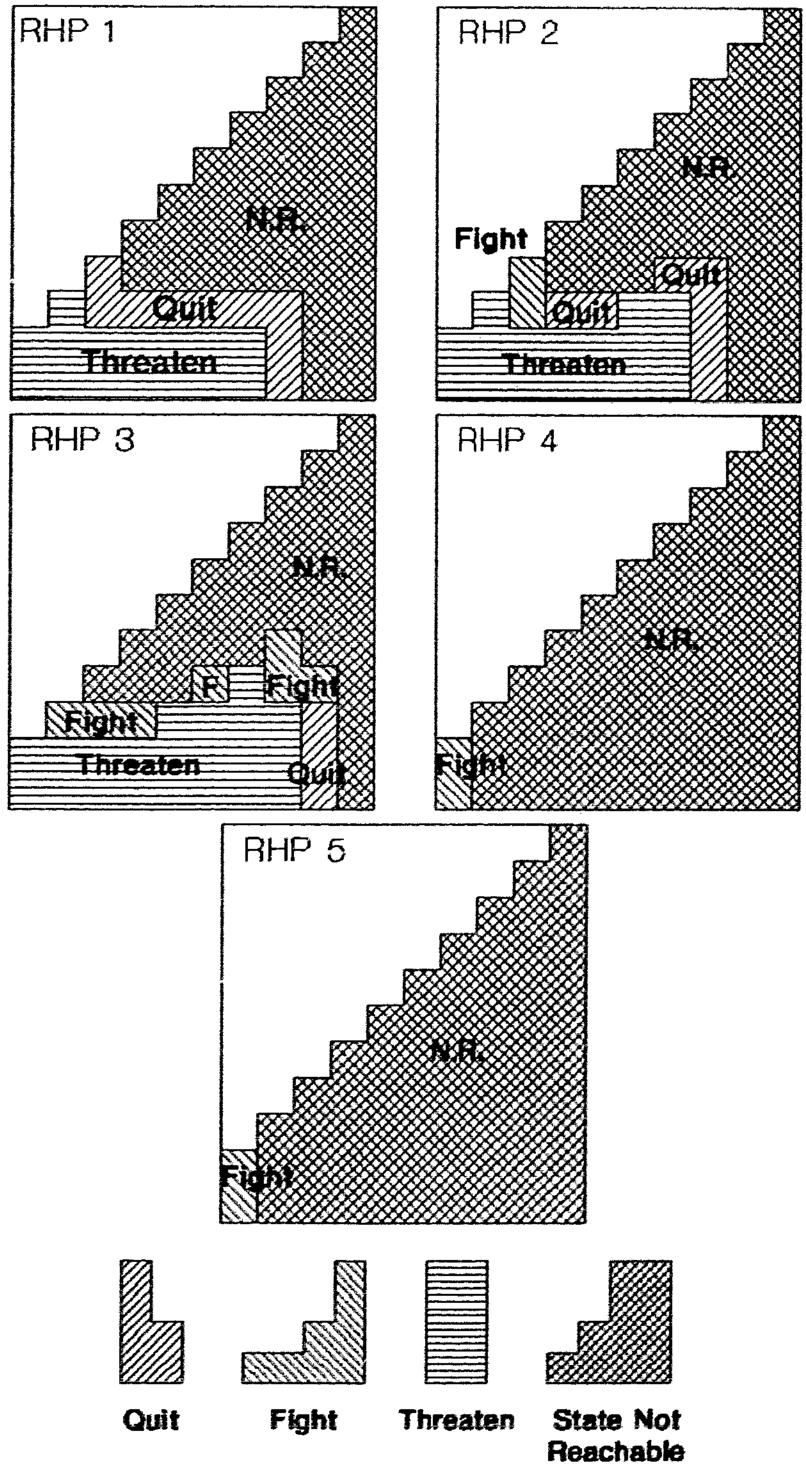
Simple model results

Solution sets for the basic model are shown in Figures 3.2 and 3.3. States in which n is greater than t are impossible, since the number of samples returned must be equal to or less than the number of threats made, which in turn cannot be higher than the number of turns. This n>t space is left white. The State Not Reachable space lies beyond a behavioural endpoint (a Quit or Fight behaviour) and is marked as "N.R.". Note that early in the contest, the optimal behaviour is Threaten, until sufficient threats are made and the optimal behaviour then becomes Quit or Fight. This seems to be a sensible result.

The expected fitnesses for the simple model are shown in Table 3.2. Not surprisingly, individuals with higher RHP expect higher fitness. The exception for RHP 5 contestant A is hard to explain. Presumably it could play the same strategy as the RHP 4 contestant A, and score higher. While there is a possibility that this result is a fault in the code, the backwards iterations do not show any signs of being faulty. It would seem any putative fault lies in the forward iterations. I can find no reason for the simple algorithms there to produce such a result.

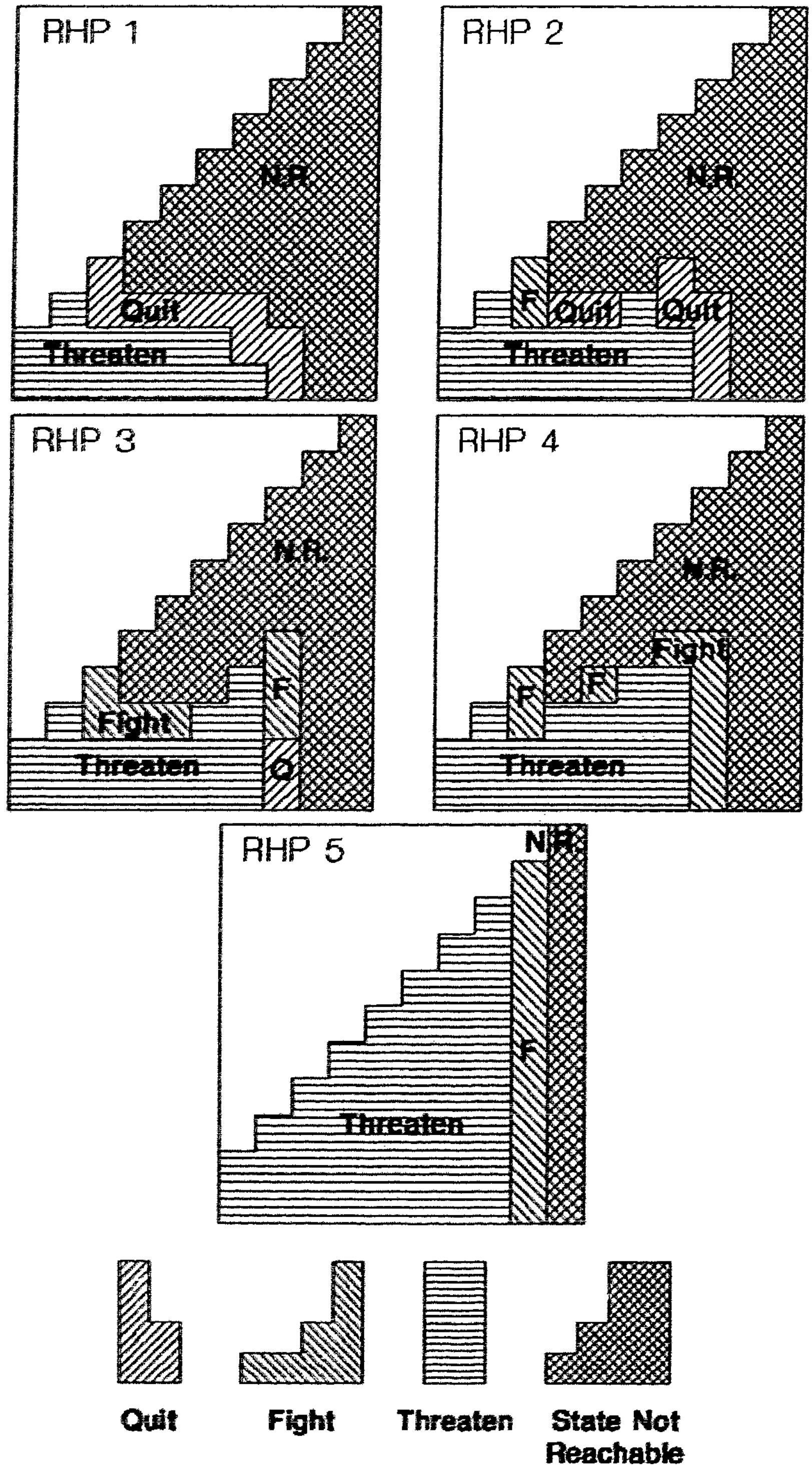
First players (A) also expected much higher

Figure 3.2 Simple model optimal behaviour sets for Contestant A



Time runs along the horizontal axis, from t=1 to T=10.
The number of fear samples returned lies on the vertical axis, from 0 to 10.
See Page 60 for further explanation of N.R. space and blank space.

Figure 3.3 Simple model optimal behaviour sets for Contestant B



Time runs along the horizontal axis, from t=1 to T=10.
The number of fear samples returned lies on the vertical axis, from 0 to 10.
See Page 60 for further explanation of N.R. space and blank space.

fitnesses than second players (B) of the same RHP. This role effect was much larger than the RHP effect. Initially one might suspect that the role effect was due to a horizon effect. Recall that the initialization procedure provided different turn 10 behavioural options to the two contestants. However, the role effect is very unlikely to be responsible for this effect since T (t=10) was not reached in any of the solutions sets (Fig 3.2, and 3.3), and turn nine was reached in only two (Contestant A, RHP 3; Fig 3.2 and Contestant B, RHP 5; Fig 3.3). Furthermore, actual inspection of the utility values (Appendix A) of states during backwards iterations show initially very similar values at t=9 diverging as t approaches 0, indicating that an initiative effect is responsible rather than a horizon effect. Contestant B must make the best of the situations A has deferred.

Table 3.2. Expected fitnesses for the simple model, by role, and RHP

Contestant 'A'		Contestant 'B'	
RHP	FITNESS	RHP	FITNESS
1	.686	1	.382
2	.688	2	.434
3	.733	3	.497
4	.780	4	.561
5	.848	5	.520

Expected fitnesses for each contestant and **RHP_e** combination. Fitness was an increasing function of RHP, with the puzzling exception of 'B' at RHP5, and strongly linked to role, with player 'A' expecting a much higher fitness.

Variable strategy model results

The optimal behaviour matrices were generally like those of the simple model. Of interest here are the expected fitnesses of various Ξ_A, Ξ_B combinations. Table 3.4 presents expected fitnesses collapsed across RHPs. Note that all RHP levels of a player are playing the same Ξ strategy. Player A consistently expects much higher fitnesses than player B, across all conditions.

The most interesting result seen in this first glance is that if ego is using strategy 1, the most clearly communicative, expected fitness is highest when the opponent is using strategy 1, for player A, and 3 for player B. Indeed the diagonal cases, when ego and opponent strategies are congruent, are not outstandingly good ones, by and large.

Player A seems to benefit from more accurate information exchange, scoring highest when the opponent provides the clearest information possible, Ξ_B1, and this information is attended to, Ξ_A3 by it's opponent. Player B on the other hand expects the highest fitness under conditions of faint information exchange, $\Xi4$, for both players.

Tables 3.5 and 3.6 present expected fitnesses by all Ξ_A, Ξ_B, RHP_e, RHP_o combinations. The methodology for solving for an ESS isn't intuitively obvious, and is probably not possible from this data. However, scrutinizing the data reveals some patterns obscured when RHP effects were ignored.

Four of the five player A RHP states expect highest fitness when the opponent is playing $\Xi 1$. Player A clearly benefits from an opponent who either provides reliable information, or who makes use of provided data. The results do not seem to support a strategy towards less use of information with higher RHP_As.

An opposite trend is seen in player B's fitnesses, in that optimal scores are expected under Ξs that seem to correlate with RHP_B. At low RHP player B expects highest fitness when the opponent is playing a non-communication strategy, and player B is closely following data provided by the opponent. This is a most curious arrangement, since player A is not making use of player B's information, the effect must be due to B's use of data from A, and yet no information is contained in that data. At higher RHPs player B's performance becomes harder to interpret.

Table 3.3. Expected fitnesses by strategy, collapsed across RHP_e

Table 3.3A Fitness Table for Mean Animal (A)

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.7406	.7336	.7355	.7350	.7339
$\Xi_A=2$	.7478	.7315	.7423	.7341	.7285
$\Xi_A=3$	**.7493**	.7380	.7450	.7284	.7302
$\Xi_A=4$	.7392	.7240	.7414	.7267	.7265
$\Xi_A=5$	.7442	.7416	.7417	.7443	.7256

Table 3.3B Fitness Table for Mean Animal (B)

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.4191	.3800	.3531	.4072	.4377
$\Xi_A=2$	.4754	.3973	.4184	.4071	.4522
$\Xi_A=3$	.5078	.4421	.4669	.4412	.5155
$\Xi_A=4$	.5030	.4345	.4653	**.5167**	.4491
$\Xi_A=5$	.4914	.4683	.4889	.4914	.4455

Note: that while these tables are collapsed across RHP, the RHP effects were weighted by **Y**, the population distribution of RHPs. Global optima are in bold font.

Table 3.4. Expected player 'A' fitnesses by strategy and RHP_e

Table 3.4A Fitness Table for (A) at RHP 1

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	**.7249**	.7068	.7094	.7083	.7026
$\Xi_A=2$	.7168	.6882	.7062	.6907	.6748
$\Xi_A=3$	.7145	.6943	.7001	.6697	.6673
$\Xi_A=4$	.6948	.6583	.6844	.6670	.6653
$\Xi_A=5$	.7169	.7039	.6726	.6759	.6670

Table 3.4B Fitness Table for (A) at RHP 2

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.7067	.6943	.6937	.6936	.6910
$\Xi_A=2$	.7131	.6875	.6986	.6938	.6766
$\Xi_A=3$	.7138	.6919	.7065	.6639	.6793
$\Xi_A=4$	.7013	.6735	.6954	.6672	.6678
$\Xi_A=5$	**.7169**	.6918	.7028	.7112	.6617

Table 3.4. Expected player 'A' fitnesses by strategy and RHP_e /cont

Table 3.4C Fitness Table for (A) at RHP 3

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.7133	.7091	.7144	.7143	.7150
$\Xi_A=2$	.7307	.7110	.7286	.7149	.7143
$\Xi_A=3$	.7338	.7231	.7323	.7200	.7178
$\Xi_A=4$	.7210	.7062	.7325	.7143	.7143
$\Xi_A=5$	.7202	.7301	.7326	**.7342**	.7143

Table 3.4D Fitness Table for (A) at RHP 4

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.7803	.7793	.7785	.7776	.7767
$\Xi_A=2$	.7815	.7803	.7794	.7790	.7783
$\Xi_A=3$	.7831	.7807	.7803	.7798	.7794
$\Xi_A=4$	.7811	.7807	.7804	.7803	.7800
$\Xi_A=5$	**.7851**	.7803	.7803	.7803	.7803

Table 3.4. Expected player 'A' fitnesses by strategy and RHP_e /cont

Table 3.5E Fitness Table for (A) at RHP 5

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.8476	.8457	.8439	.8421	.8403
$\Xi_A=2$	.8488	.8476	.8463	.8450	.8438
$\Xi_A=3$	**.8492**	.8484	.8476	.8468	.8460
$\Xi_A=4$	.8487	.8483	.8479	.8476	.8472
$\Xi_A=5$	.8475	.8476	.8476	.8476	.8476

Table 3.5. Expected player 'B' fitnesses by strategy and RHP_e

Table 3.5A Fitness Table for (B) at RHP 1

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.5227	.4681	.3461	.3772	.3923
$\Xi_A=2$	.4772	.4928	.5303	.4375	.3714
$\Xi_A=3$	.5344	.4642	.5316	.4261	.4859
$\Xi_A=4$	.5245	.4704	.5675	.4373	.3493
$\Xi_A=5$	**.6146**	.5071	.5686	.5697	.3414

Table 3.5B Fitness Table for (B) at RHP 2

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.4028	.3161	.3086	.3322	.3251
$\Xi_A=2$	.4395	.3254	.3436	.2956	.3728
$\Xi_A=3$	.4505	.3834	.3693	.3315	.3466
$\Xi_A=4$	.4425	.3485	.3606	.4420	.3711
$\Xi_A=5$	**.4840**	.4036	.4005	.3964	.3653

Table 3.5. Expected player 'B' fitnesses by strategy and RHP_e /cont

Table 3.5C Fitness Table for (B) at RHP 3

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.3587	.3075	.2996	.3526	.4361
$\Xi_A=2$	.4824	.3318	.3491	.3148	.3968
$\Xi_A=3$	.5320	.4371	.4391	.3737	**.5394**
$\Xi_A=4$	.5120	.4136	.3995	.5061	.3952
$\Xi_A=5$	.4438	.4484	.4370	.4342	.3912

Table 3.5D Fitness Table for (B) at RHP 4

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.4859	.4824	.4226	.4838	.4740
$\Xi_A=2$	.5130	.4990	.4923	.4806	.5880
$\Xi_A=3$	.5182	.4709	.5322	**.5907**	.5880
$\Xi_A=4$	.5479	.4869	.5630	.5890	.5880
$\Xi_A=5$	.5657	.5142	.5690	.5873	.5880

Table 3.5. Expected player 'B' fitnesses by strategy and RHP_e /cont

Table 3.5E Fitness Table for (B) at RHP 5

	$\Xi_B=1$	$\Xi_B=2$	$\Xi_B=3$	$\Xi_B=4$	$\Xi_B=5$
$\Xi_A=1$	.4564	.5026	.5237	.6525	.6422
$\Xi_A=2$	.4424	.5042	.5852	**.8220**	.6422
$\Xi_A=3$	.4780	.5001	.5777	.6462	.6422
$\Xi_A=4$	.4768	.5493	.6398	.6431	.6422
$\Xi_A=5$	.4250	.5470	.6337	.6400	.6422

CONCLUSION

The model shows quite clearly a significant effect of role. The contestant who makes the first move can expect a much higher payoff. This was not an anticipated result, since no real role asymmetry was incorporated into the model. While empirical studies consistently find role effects in agonistic encounters (Tinbergen, 1953; Burges, 1976; Davies, 1978; Krebs, 1982; Desrochers & Hannon, 1989), these roles are due to external factors. The players A and B are symmetrical in all but behaviour sequence. The surprisingly strong role effect is hard to interpret with respect to empirical work.

Maximum expected fitnesses were returned in many cases under conditions of information exchange. However, the global optima in Tables 3.5 and 3.6 are not to be weighted too heavily, as the expected fitness is highly sensitive to opponent strategy. This is a result of the programming decision to use ego's Ψ to interpret the opponents actions, the value of communicating and the value of assessing the opponents signals become completely inseparable. As a quick patch, it would be tempting to calculate the mean payoff for a given $\mathbf{RHP}_e$ and Ξ_e collapsed across $\mathbf{RHP}_o$ and Ξ_o. Unfortunately, this would be meaningless since ego isn't playing against a population distribution of Ξ_o strategies.

The problem of how to solve for opponent Ξ functions different from that of the opponent is a subtle and stubborn one. Ideally a population distribution of ego and opponent functions would be solved to an RHP and role specific ESS set. Solving against a Ξ function other than the ego's own requires a known population distribution. This was not attempted since no defensible a priori function presented itself. It would be possible to loop through the whole procedure using the mean fitnesses as a weighting factor in a sort of 'intergenerational' simulation hopefully converging on an ESS. This would be both highly inelegant and time consuming.

It is reasonable to assume that optimal Ξ strategies would be condition dependent on RHP. Simulations using a separate Ξ for each $\mathbf{RHP_e}$ and $\mathbf{RHP_o}$ were run. In essence the 1x5 Ξ function was replaced by a 5x5 Ξ matrix. Each of the columns of the matrix was one of the five Ξ functions from Fig 3.1. Each possible contestant A and contestant B matrix was played against each other. The algorithm needed to analyze the 22Meg fitnesses output file would probably be much more complicated than the one used to generate it.

CHAPTER 4

SUMMARY AND SYNTHESIS

In Chapter 2, I presented data showing evidence for aggressive communication of intentions between American Coots, but found no correlation between risk and effectiveness between various displays. I suggest that the apparent failure to show a bid/cost relationship in aggressive behaviours in this species is due to the combined effects of often repeated encounters between the same individuals, and the establishment of dear enemy (Getty, 1987) effects. The former problem obscures the clear RHP versus the aggressiveness communication dichotomy present in stranger vs. stranger, non-divisible, resource studies. The absence of a model of behaviour under circumstances other than these, leaves a great range, perhaps even the majority, of aggressive behaviour unexplained. Besides immediate actions and RHP, repeat encounters allow the communication of aggressiveness, the general tendency to escalate, to be communicated. Communication of this third quantity has been closely associated with work on badges of status (Rohwer, 1977, 1982; Rohwer & Rohwer, 1978; Studd & Robertson, 1985a&b). Clearly, a model linking this subject with repeated contests over divisible resources is required before a more coherent analysis can be made of the sort of data presented here.

In Chapter 3, I presented a game in which contestants varied in how likely they are to provide information about their estimates of relative fighting ability. van Rhijn & Vodegel's (1980) model, to the best of my knowledge, most resembles the one presented above. van Rhijn & Vodegel's model, comprised of a series of turns in which opponents either Retreat, use Conventional displays, or escalate to Dangerous fighting, appears like the model presented above, but major differences exist. van Rhijn & Vodegel's model addressed communication of intention to attack, not communication about RHP, but more importantly, their model included the recognition of individuals from previous encounters. While very few models of aggressive communication incorporate individual recognition, encounters between known individuals is probably the case in most agonistic encounters in many species (van Rhijn, 1980). In comparison, van Rhijn & Vodegel's model and my own model are quite difficult, since the former is a model of communication of intentions, while the later deals with communication of ability.

The results presented in this thesis do not go very far towards presenting a satisfying answer to the question of communication in aggressive conflicts. But I think I have accurately described the difficulties in answering such a broad and vague, yet complicated, question. What I have done is to develop some of the issues that will require further formal study before the topic can be truly understood. A set of formulae describing precisely the behaviours seen in the field will probably never be assembled, much less understood. But this is not the value of modelling in behavioural ecology. In the case of agonistic communication, great advances in understanding have been made by the application of very basic game theoretic principles. The initial Hawk-Dove, and War of Attrition games are very simple, but their power of explanation is proportionately strong. By exceeding their scope, by violating their assumptions, we reveal distinctions, assumptions, and issues that were previously blurred, or unnoticed. I hope to have demonstrated some of the areas where effort can be used constructively by pointing out where current theory ends.

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APPENDIX 1

STATE UTILITIES FOR BASIC MODEL

These numbers are the cell utilities calculated during the backwards iterations of the simple model. Utility is listed for each state regardless of whether or not the cell can be reached during forwards iterations.

The format is: Contestant@ rhp(RHP), t(Turn), n(Samples Returned) = Utility

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A@ rhp(1) t(1) n(0) = 7.50128278856209E-0001
A@ rhp(1) t(1) n(1) = 7.35240247902766E-0001

A@ rhp(1) t(2) n(0) = 7.46017573767858E-0001
A@ rhp(1) t(2) n(1) = 7.15875235225212E-0001
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A@ rhp(1) t(7) n(3) = 6.66999999400105E-0001
A@ rhp(1) t(7) n(4) = 6.66999999400105E-0001
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A@ rhp(1) t(7) n(7) = 6.82536711183275E-0001

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A@ rhp(1) t(8) n(2) = 6.66999999300060E-0001
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A@ rhp(4) t(9) n(8) = 8.48338503391460E-0001
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A@ rhp(5) t(3) n(1) = 8.11499221064878E-0001
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A@ rhp(5) t(5) n(2) = 8.19018246982523E-0001
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A@ rhp(5) t(6) n(4) = 8.39907042278355E-0001
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B@ rhp(4) t(8) n(3) = 7.32853399085798E-0001
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B@ rhp(4) t(8) n(7) = 8.39823165812049E-0001
B@ rhp(4) t(8) n(8) = 8.65359061712297E-0001
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B@ rhp(5) t(1) n(0) = 1.42847128218455E+0000
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B@ rhp(5) t(3) n(2) = 9.72061048639262E-0001
B@ rhp(5) t(3) n(3) = 9.98188896244756E-0001

B@ rhp(5) t(4) n(0) = 8.34618165951724E-0001
B@ rhp(5) t(4) n(1) = 8.62623397914831E-0001
B@ rhp(5) t(4) n(2) = 9.07719536347940E-0001
B@ rhp(5) t(4) n(3) = 9.83922387885286E-0001
B@ rhp(5) t(4) n(4) = 1.10261713880755E+0000

B@ rhp(5) t(5) n(0) = 7.96488947883518E-0001
B@ rhp(5) t(5) n(1) = 8.20943379457276E-0001
B@ rhp(5) t(5) n(2) = 8.47243308579891E-0001
B@ rhp(5) t(5) n(3) = 8.82087076077369E-0001
B@ rhp(5) t(5) n(4) = 9.31037452415694E-0001
B@ rhp(5) t(5) n(5) = 9.99282344125277E-0001

B@ rhp(5) t(6) n(0) = 7.68863568543566E-0001
B@ rhp(5) t(6) n(1) = 7.91690740887134E-0001
B@ rhp(5) t(6) n(2) = 8.16067833364286E-0001
B@ rhp(5) t(6) n(3) = 8.44343365226450E-0001
B@ rhp(5) t(6) n(4) = 8.86140775781314E-0001
B@ rhp(5) t(6) n(5) = 9.53849571043065E-0001
B@ rhp(5) t(6) n(6) = 1.05642075558171E+0000
```

```
B@ rhp(5) t(7) n(0) = 7.46001742320914E-0001
B@ rhp(5) t(7) n(1) = 7.65790177949384E-0001
B@ rhp(5) t(7) n(2) = 7.91763507661926E-0001
B@ rhp(5) t(7) n(3) = 8.22102047171938E-0001
B@ rhp(5) t(7) n(4) = 8.55386647864179E-0001
B@ rhp(5) t(7) n(5) = 8.94157982646902E-0001
B@ rhp(5) t(7) n(6) = 9.45612487289509E-0001
B@ rhp(5) t(7) n(7) = 1.01171924502887E+0000

B@ rhp(5) t(8) n(0) = 7.33909925660555E-0001
B@ rhp(5) t(8) n(1) = 7.46191247789284E-0001
B@ rhp(5) t(8) n(2) = 7.63274857334181E-0001
B@ rhp(5) t(8) n(3) = 7.85377891646931E-0001
B@ rhp(5) t(8) n(4) = 8.11928516432090E-0001
B@ rhp(5) t(8) n(5) = 8.43524646974402E-0001
B@ rhp(5) t(8) n(6) = 8.86407222606067E-0001
B@ rhp(5) t(8) n(7) = 9.54215613708584E-0001
B@ rhp(5) t(8) n(8) = 1.04994851064657E+0000

B@ rhp(5) t(9) n(0) = 7.27761067955726E-0001
B@ rhp(5) t(9) n(1) = 7.37212826852556E-0001
B@ rhp(5) t(9) n(2) = 7.50612763786194E-0001
B@ rhp(5) t(9) n(3) = 7.68428402351674E-0001
B@ rhp(5) t(9) n(4) = 7.90035846073806E-0001
B@ rhp(5) t(9) n(5) = 8.13748729216968E-0001
B@ rhp(5) t(9) n(6) = 8.38144771362749E-0001
B@ rhp(5) t(9) n(7) = 8.63628960190908E-0001
B@ rhp(5) t(9) n(8) = 8.91538860643777E-0001
B@ rhp(5) t(9) n(9) = 9.19075685594180E-0001
```

APPENDIX 2

BAYESIAN BOXERS MODEL CODE

```
program boxers6;
{                                                                           }
{                                                                           }
{                           Bayesian Boxers VI A                            }
{                                                                           }
{    This is version 6A,    a symmetrical game with two combatants          }
{                           and forwards iterated expected fitness          }
{                           NB two opponants use different PSI stategies    }
{                           Pr(fear) is a fn of est assymmetry              }
{                           Est. opp n using my Strategy                    }
{                                                                           }
{                                                                           }
{       Copyright 1992      Peter L. Hurd                                   }
{                           Simon Fraser University                         }
{                           Department of Biological Sciences               }
{                           Behavioural Ecology Research Group              }
{                           Burnaby B.C. V5A 1S6                            }
{                           Canada                                          }
{                                                                           }
{                                                                           }
{                                                                           }

uses Crt;

const
        RHP_i=5;
        endT=10;

type
        _i=array[1..RHP_i] of real;             {absolute RHPs}
        _a=array[-RHP_i+1..RHP_i-1] of real;    {assymmetry of RHPs}
        Fs=array[0..endT+1,1..RHP_i] of real;   {utility matrices}
        ARISTOS=array [1..endT,0..endT+1,1..RHP_i] of char; {solution sets}
```

```
        PSI_i=array[-4..4] of real;                 {Pr. show fear}

var
        A,C,D: text;                                {input/output variables}
        AGAIN: boolean;                             {looping variable}
        RESP,V,B_OPP,B_ME: char;
        j,i,t,n,n_o,MAXn,BMAX,tc,TEMP,RHP_e,ALTERNATE,
         A_TURN,S,S_a,S_b: integer;
        NOMINATOR,PARTDENOM,DENOMINATOR,VMAX,THIS_i,THIS_no,
         EXPR,BVAL,Dc,Prn_o,SUM,T2,T3,T4,T5,VAL,Pr_here,PSI,
         M,Vr,Vk:real;
        Y: _i;                                      {pop. dist & prior fn}
        PSI_a,PSI_b:PSI_i;                          {Pr. show fear}
        w,z: _a;                          {pr injury & pr win as fn of assymmetry}
        B: array [1..3] of real;          {B[b] is utility of behaviour b}
        F0_a,F1_a,F0_b,F1_b: Fs;                    {utility matrices}
        ARIST_A,ARIST_B: ARISTOS;                   {solution sets}
        FIT_e:array [1..RHP_i] of real;   {expected fitness output matrix}
        STRATEGY:array[1..5,-4..4] of real;         {PSI library}

function FACTORIAL (j:integer):longint; {calculates factorials}
var a: integer;
    PROD: longint;
begin
 PROD:=1;
 if j>1 then for a:=1 to j do PROD:=PROD*a;
 FACTORIAL:=PROD;
end;

procedure WAIT; {a pause function, used during debugging & development}
begin
 writeln('press any key to continue');
 while KeyPressed=false do;
```

```
 RESP:=ReadKey;
end;

Function Power(x,y:real):real; {from Timo Salmi pascal function library}
Begin
  If y=0 Then
    power:=1.0
  Else if x=0 Then
    Power:=0.0
  Else If x>0 Then
    Power:=exp(y*ln(x))
  Else if Trunc(y) mod 2=0 Then
    Power:=exp(y*ln(abs(x)))
  Else
    Power:=-exp(y*ln(abs(x)));
End;

function CHOOSE(a,b:integer):real; {calculates binomial a choose b}
begin
 CHOOSE:=FACTORIAL(a)/(FACTORIAL(b)*FACTORIAL(a-b));
end;

procedure FILE_SETUP; {opens & prepares output files}
begin
 assign(A, 'C:\MISC\PLAYGRND\BOX6ARST.TXT');
 assign(C, 'C:\MISC\PLAYGRND\BOX6FITS.TXT');
 assign(D, 'C:\MISC\PLAYGRND\BOX6PSIS.TXT');
 rewrite(A); rewrite(C); rewrite(D);
end;

procedure FILE_CLOSE; {closes output files}
begin
 writeln(A,'FILE COMPLETE - SUCCESSFUL RUN');
```

```
 writeln(C,'FILE COMPLETE - SUCCESSFUL RUN');
 writeln(D,'FILE COMPLETE - SUCCESSFUL RUN');
 close(A); close(C); close(D);
 writeln('check out the results and such in C:\MISC\PLAYGRND\BOX6****.TXT');
end;

{**************************************************************************}
{             end of procedures, functions and file management shtick      }
{             start of greeting, set-up and backwards iteration noise      }
{**************************************************************************}

procedure WELCOME;   {greet and insult the user}
begin
 ClrScr;
 writeln('Bayesian Boxers VI   ');
 writeln;
 writeln('    This is version six, a symmetrical game with two combatants, ');
 writeln('                          forwards iterated expected fitness,     ');
 writeln('                          overhead cams, driver side airbags,     ');
 writeln('                          fuzzy dice, and rusted-out axels        ');
 writeln;
 writeln('Peter L. Hurd                                   ');
 writeln('Simon Fraser University                         ');
 writeln('Department of Biological Sciences               ');
 writeln('Behavioural Ecology Research Group              ');
 writeln('Burnaby B.C. V5A 1S6                            ');
 writeln(' Canada                                          ');
 writeln;
 writeln;
 writeln('Enter A for another run');
 writeln('  or  Q to quit, use CAPS!!!');
 readln(V);
 if V='A' then begin
```

```
  write('enter Vk  - 0.333 - ');
  readln(Vk);
  write('enter Vr  - 0.667 - ');
  readln(Vr);
  tc:=0;
 end;
 if V='Q'
 then begin
  AGAIN:=false;
  writeln('here s the data, calculator broken lazy guy?');
  end
 else begin
  write('now enter Dc    - 0 - ');
  readln(Dc);
  if Dc<0.0000000001 then begin
   Dc:=0.0000000001;
   writeln('enforcing minimum Dc of 0.0000000001');
  end;
 end;
end;

procedure FLUFF; {fill parameter matrices, and prompt the user unnecessarily}
begin
 writeln('setting up the shtick');
 Y[1]:=0.1; Y[2]:=0.2; Y[3]:=0.4; Y[4]:=0.2; Y[5]:=0.1;   {Y is pop (& prior) dist of RHP}

w[-4]:=0.3;w[-3]:=0.25;w[-2]:=0.2;w[-1]:=0.2;w[0]:=0.15;w[1]:=0.1;w[2]:=0.05;w[3]:=0.02;w[
4]:=0.01;
 for i:=-4 to 4 do begin
  z[i]:=(i+5)/10;
 end;
 M:=0.1;
 for S:=1 to 5 do begin
```

```
  j:=0;
  for i:=-4 to 4 do begin
   STRATEGY[S,i]:=S/10+j*M;
   j:=j+1;
  end;
  M:=M-0.025;
 end;
 WELCOME;
end;

procedure SETUP_B; {fill the ARISTOS matrices with garbage}
begin
 for t:=1 to endT do begin
  for n:=0 to endT do begin
   for RHP_e:=1 to RHP_i do begin
    ARIST_a[t,n,RHP_e]:='-';
    ARIST_b[t,n,RHP_e]:='-';
   end;
  end;
 end;
end;

procedure READ_PSIs; {reads in new psi from library as per strategy S_x}
begin
 for i:=-4 to 4 do begin
  PSI_a[i]:=STRATEGY[S_a,i];
  PSI_b[i]:=STRATEGY[S_b,i];
 end;
end;

procedure BAYES; {calclates bayesian estimate of pr opponant RHP}
begin
 if A_TURN=1 then PSI:=PSI_a[RHP_e-i] else PSI:=PSI_b[RHP_e-i];
```

```
 NOMINATOR:=Y[i]*CHOOSE(t,n)*POWER(PSI,n)*POWER(1-PSI,t-n);
 DENOMINATOR:=0;
 for j := 1 to RHP_i do begin
  if A_TURN=1 then PSI:=PSI_a[RHP_e-j] else PSI:=PSI_b[RHP_e-j];
  PARTDENOM:=CHOOSE(t,n)*POWER(PSI,n)*POWER(1-PSI,t-n)*Y[j];
  DENOMINATOR:=DENOMINATOR+PARTDENOM;
 end;
 EXPR:=NOMINATOR/DENOMINATOR;    {EXPR is Pr RHP=RHP_i given t&n}
end;

procedure INITIALIZE_B;    {initialize f1_b, that's player B and such}
begin
 writeln('initializing f1 for reward schedule ',V,', please be cool');
 t:=endT;
 for RHP_e:=1 to RHP_i do begin
  for n:=0 to endT+1 do begin
   F0_a[n,RHP_e]:=0;
   F1_a[n,RHP_e]:=0;
   F0_b[n,RHP_e]:=0;
   F1_b[n,RHP_e]:=0;
   for i:=1 to RHP_i do begin
    BAYES;
    THIS_i:=EXPR*(1-w[RHP_e-i])*(Vr+z[RHP_e-i]*Vk)-(t-1)*Dc;
    F1_a[n,RHP_e]:=F1_a[n,RHP_e]+THIS_i;
    F1_b[n,RHP_e]:=F1_b[n,RHP_e]+THIS_i;
   end;
   if F1_b[n,RHP_e]>Vr
   then ARIST_B[t,n,RHP_e]:='F'
   else begin                    {note last turn, options fight & quit only}
    F1_b[n,RHP_e]:=Vr-(t-1)*Dc;
    ARIST_B[t,n,RHP_e]:='Q';
   end;
  end;
```

```
 end;
end;

procedure INITA_Bs;  {calculates utility for last turn}
begin
 B[1]:=B[1]+EXPR*Prn_o*Vr; {utility for A if quit on last turn}
  {next two lines calculate utility for A if threaten on last turn}
 if B_OPP='Q' then B[2]:=B[2]+EXPR*Prn_o*(Vr+Vk-t*Dc); {if B quit this turn}
 if B_OPP='F' then B[2]:=B[2]+EXPR*Prn_o*(1-w[RHP_e-i])*(Vr+z[RHP_e-i]*Vk)-t*Dc; {if B B
fight this turn}
  {next line calculates utility for A if fight on last turn}
 B[3]:=B[3]+EXPR*Prn_o*(1-w[RHP_e-i])*(Vr+z[RHP_e-i]*(Vk-(t-1)*Dc));
end;

procedure NEXTB_INIT;      { calculates the pr that opp is of state n     }
begin                      { & finds opponants next behaviour based on it}
 if A_TURN=1 then PSI:=PSI_a[RHP_e-i] else PSI:=PSI_b[RHP_e-i]; {both these options get
used WHY!?}
 Prn_o:=CHOOSE(t,n_o)*POWER(PSI,n_o)*POWER(1-PSI,t-n_o);
 B_OPP:=ARIST_B[t,n_o,i];
end;

procedure INITIALIZE_A;   {initialize f1_a and such}
begin
 for RHP_e:=1 to RHP_i do begin
  for n:=0 to endT+1 do begin
   B[1]:=0;B[2]:=0;B[3]:=0;
   for i:=1 to RHP_i do begin
    BAYES;
    for n_o:=1 to endT+1 do begin
     NEXTB_INIT;
     INITA_Bs;
    end;      {end of n_o loop}
```

```
   end;        {end of i loop}
   VMAX:=0;BMAX:=0;
   for j:=1 to 3 do begin
    if B[j]>VMAX then begin
     VMAX:=B[j];
     BMAX:=j;
    end;
   end;
   if BMAX=1 then ARIST_A[t,n,RHP_e]:='Q';
   if BMAX=2 then ARIST_A[t,n,RHP_e]:='T';
   if BMAX=3 then ARIST_A[t,n,RHP_e]:='F';
   F1_a[n,RHP_e]:=VMAX;  {Im guessing this is RHP_e & not i}
  end;         {end of n loop}
 end;          {end of RHP_e loop}
 A_TURN:=-1;
 writeln('f1 now fully funkified');
end;

{********************************************************************}
{*  end of initializing proceedures * start of backwards iterations *}
{********************************************************************}

procedure QUIT;          {calculate utility of quitting}
begin
 B[1]:=Vr;
end;

procedure NEXTB_B; {calculate pr opp is at state n, & find opp next behav}
begin
 if A_TURN=1 then PSI:=PSI_a[RHP_e-i] else PSI:=PSI_b[RHP_e-i];
 Prn_o:=CHOOSE(t,n_o)*POWER(PSI,n_o)*POWER(1-PSI,t-n_o);
 if A_TURN=1
 then B_OPP:=ARIST_B[t,n_o,i]
```

```
 else B_OPP:=ARIST_A[t+1,n_o,i];
end;

procedure OPP_THREAT; {calculate utility of T if opp also does T after}
begin
 if A_TURN=1 then PSI:=PSI_b[RHP_e-i] else PSI:=PSI_a[RHP_e-i];
 T2:=PSI;
 if A_TURN=1 then T3:=F1_a[n+1,i] else T3:=F1_b[n+1,i];
 T4:=1-PSI;
 if A_TURN=1 then T5:=F1_a[n,i] else T5:=F1_b[n,i];
 THIS_no:=(T2*T3+T4*T5)-t*Dc;
end;

procedure OPP_QUIT; {calc util of T if opp does Q after}
begin
 THIS_no:=Vr+Vk-t*Dc;
end;

procedure OPP_FIGHT; {calc util of T if opp does F next}
begin
 T2:=1-w[RHP_e-i];
 T3:=Vk-t*Dc;
 THIS_no:=T2*(z[RHP_e-i]*(T3+Vr)+(1-z[RHP_e-i])*Vr);
end;

procedure THREATEN; {calc expected util of T}
begin
 BVAL:=0;
 for i:=1 to RHP_i do begin       {loop through opp RHP, aka i, states}
  THIS_i:=0;
  if A_TURN=1 then MAXn:=t else MAXn:=t+1;
  SUM:=0;
  for n_o := 0 to MAXn do begin   {loop through opp n states}
```

```
   NEXTB_B;
   if B_OPP='T'then OPP_THREAT;
   if B_OPP='Q' then OPP_QUIT;
   if B_OPP='F' then OPP_FIGHT;
   THIS_i:=THIS_i+Prn_o*THIS_no;  {summate partial utility by pr of n state}
  end;                        {next n_o}
  BAYES;
  BVAL:=BVAL+THIS_i*EXPR;         {summate partial utility by pr of i state}
 end;                    {next i}
 B[2]:=BVAL;
end;

procedure FIGHT;         {calculate utility of fighting}
var T1, T2, T3, T4: real;
begin
 BVAL:=0;
 for i:=1 to RHP_i do begin
  BAYES;
  T1:=EXPR;
  T2:=1-w[RHP_e-i];
  T3:=z[RHP_e-i];
  T4:=Vk-(t-1)*Dc;
  THIS_i:=T1*T2*((T3*T4)+Vr);
  BVAL:=BVAL+THIS_i;
 end;
 B[3]:=BVAL;
end;

procedure CALCULATE;    {compare utility of behaviours}
begin
 QUIT;           {find value of B[1]}
 THREATEN;       {find value of B[2]}
 FIGHT;          {find value of B[3]}
```

```
 VMAX:=0;
 BMAX:=0;
 for j:=1 to 3 do begin
  if B[j]>VMAX then begin
   VMAX:=B[j];
   BMAX:=j;
  end;
 end;
 if A_TURN=1
 then begin
  if BMAX=1 then ARIST_A[t,n,RHP_e]:='Q';
  if BMAX=2 then ARIST_A[t,n,RHP_e]:='T';
  if BMAX=3 then ARIST_A[t,n,RHP_e]:='F';
  F0_a[n,RHP_e]:=VMAX;
 end
 else begin
  if BMAX=1 then ARIST_B[t,n,RHP_e]:='Q';
  if BMAX=2 then ARIST_B[t,n,RHP_e]:='T';
  if BMAX=3 then ARIST_B[t,n,RHP_e]:='F';
  F0_b[n,RHP_e]:=VMAX; {is this *i* or what?}
 end;
end;

procedure SWAP_B;      {switching F0 to F1 for next t}
begin
 for RHP_e:=1 to RHP_i do begin
  for n:=0 to endT do begin
   F1_a[n,RHP_e]:=F0_a[n,RHP_e];
   F1_b[n,RHP_e]:=F0_b[n,RHP_e];
  end;
 end;
end;
```

```
procedure BACKWARDS;    {backwards iterations, from endT to t=1}
begin
 SETUP_B;
 INITIALIZE_B;
 INITIALIZE_A;     {funkify the F1 matrix}
 writeln('starting backwards iterations');
 write('thinking');
 for t:=endT-1 downto 1 do begin
  for ALTERNATE:=1 to 2 do begin
   for RHP_e:=1 to RHP_i do begin
    for n:=0 to t do begin
     CALCULATE;    {which means do the DPE, basically}
    end;           {end of the n loop}
   write('.');
   end;            {end of the RHP_e loop}
   A_TURN:=A_TURN*-1;
  end;             {end of the alternate loop}
  SWAP_B;          {switch F0 matrix over to F1}
 end;              {end of the t loop}
end;

{ * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *}
{  END OF THE BACKWARDS ITERATION MECHANISM                         }
{         forwards iterating, from now on F0_a is Pr(n) now         }
{                                         F1_a is Pr(n) next turn }
{ * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *}

procedure CLEAR_SHIT; {rem statement of astounting helpfulness}
begin
 ClrScr;
 writeln;
end;
```

```
procedure SETUP_F; {set up the thing written four lines down}
begin
 writeln;
 writeln('now starting forwards iterations to calcuate expected fitnesses');
 for RHP_e:=1 to RHP_i do begin
  FIT_e[RHP_e]:=0;
  F1_a[0,RHP_e]:=1;F0_a[0,RHP_e]:=0;
  for n:=1 to endT+1 do begin
   F0_a[n,RHP_e]:=0;F1_a[n,RHP_e]:=0;
  end;
 end;
end;

procedure SWAP_F; {F0_a is Pr(n) now,  F1_a is Pr(n) next turn}
begin
 for n:=0 to t do begin
  F0_a[n,RHP_e]:=F1_a[n,RHP_e];
  F1_a[n,RHP_e]:=0;
  if F0_a[n,RHP_e]=0
  then if A_TURN=1
   then ARIST_A[t,n,RHP_e]:='*'
   else ARIST_B[t,n,RHP_e]:='*';
 end;
end;

procedure NEXTB_F; {get ego's next behaviour is}
begin
 if A_TURN=1
 then B_ME:=ARIST_A[t,n,RHP_e]
 else B_ME:=ARIST_B[t,n,RHP_e];
end;

procedure ADD_IT_UP; {exp util=sum of pr density state locus + state utility}
```

```
begin
 FIT_e[RHP_e]:=FIT_e[RHP_e]+Pr_here*VAL;
end;

procedure QUIT_F; {set cell utility if ego quits}
begin
 VAL:=Vr;
 Pr_here:=F0_a[n,RHP_e];
 ADD_IT_UP;
end;

procedure THREAT_F; {set cell utility if ego threatens}
begin
 for i:=1 to RHP_i do begin {loop through opp RHP}
  BAYES;
  for n_o:=0 to t do begin  {loop through opp n states}
   VAL:=0;
   if A_TURN=1 then PSI:=PSI_b[RHP_e-i] else PSI:=PSI_a[RHP_e-i]; {NOTE HERE !!!!}
   Prn_o:=CHOOSE(t,n_o)*POWER(PSI,n_o)*POWER(1-PSI,t-n_o);
   Pr_here:=EXPR*F0_a[n,RHP_e]*Prn_o;
   if Pr_here=0 then writeln('!');
   if t=0 then B_OPP:='T' else if A_TURN=1 then B_OPP:=ARIST_B[t,n_o,i] else
B_OPP:=ARIST_A[t,n_o,i];
   if B_OPP='Q' then VAL:=Vr+Vk-t*Dc;         {Fixed this line}
   if B_OPP='T' then begin
    F1_a[n+1,RHP_e]:=F1_a[n+1,RHP_e]+Pr_here*PSI;   {inc in N+1 cell utility iff Psi T}
    F1_a[n,RHP_e]:=F1_a[n,RHP_e]+Pr_here*(1-PSI);   {inc in N cell utility iff Psi F  }
   end;
   if B_OPP='F' then VAL:=(1-w[RHP_e-i])*(Vr+z[RHP_e-i]*Vk);
   ADD_IT_UP;
  end;          {next n_o}
 end;           {end of i loop}
end;
```

```
procedure FIGHT_F; {set cell utility if ego fights}
begin
 for i:=1 to RHP_i do begin
  BAYES;
  for n_o:=0 to t do begin
   VAL:=0;
   if A_TURN=1 then PSI:=PSI_b[RHP_e-i] else PSI:=PSI_a[RHP_e-i];
   Prn_o:=CHOOSE(t,n_o)*POWER(PSI,n_o)*POWER(1-PSI,t-n_o);
   Pr_here:=EXPR*F0_a[n,RHP_e]*Prn_o;
   VAL:=(1-w[RHP_e-i])*(Vr+z[RHP_e-i]*Vk);
   ADD_IT_UP;
  end;          {next n_o}
 end;           {end of i loop}
end;

procedure WRITE_F; {blast data out to disk}
begin
 writeln(C);
 writeln (C,'PSI_a=',S_a,' PSI_b=',S_b);
 if A_TURN=1 then write(C,'Actor A ') else write(C,'Actor B ');
 writeln(C,'RHP(ego) is ',RHP_e);
 writeln(C,'Vk structure is ',V);
 writeln(C,'Where Vk=',Vk,' Vr=',Vr,' tc=',tc);
 writeln(C,'and Dc=',Dc);
 write(C,'maximum fitness is ');
 if V='A' then writeln(C,Vr+Vk) else writeln(C,'endT+Vr');
 for RHP_e:=1 to RHP_i do begin
  writeln(C,'expected fitness for RHP(ego) of ', RHP_e,' is ',FIT_e[RHP_e]);
 end;
 writeln(C,'mean fitness is
',0.1*FIT_e[1]+0.2*FIT_e[2]+0.4*FIT_e[3]+0.2*FIT_e[4]+0.1*FIT_e[5]);
end;
```

```
procedure FORWARDS; {  calculating the expected fitness for each contestant }
begin               {  for each RHP(ego)                                     }
 A_TURN:=1;
 CLEAR_SHIT;
 for ALTERNATE:=1 to 2 do begin
  SETUP_F;
  writeln; write('thinking..., again');
  for RHP_e:=1 to RHP_i do begin
   for t:=0 to endT do begin
    SWAP_F;      {diddling about with the  F1-F0 nonsense}
    write('.');
    for n:=0 to t do begin
     VAL:=0;
     if t=0 then B_ME:='T' else NEXTB_F;
     if B_ME='Q' then QUIT_F;
     if B_ME='T' then THREAT_F;
     if B_ME='F' then FIGHT_F;
    end;         {end of the n loop}
   end;          {end of the t loop}
  end;           {end of the RHP_E loop}
  WRITE_F;       {pipe wisdom to disk}
  A_TURN:=A_TURN*-1;
 end;            {end of alternate loop}
end;

{*******************************************************************}
{        end of forwards iterations, start of print-out routines    }
{*******************************************************************}

procedure PRNTARIS;     {print out the ARISTOS matrix}
begin
 writeln(A); writeln(D);
 A_TURN:=1;
```

```
 writeln (D,'PSI_a=',S_a,' PSI_b=',S_b);
 for ALTERNATE:=1 to 2 do begin
  for i:=-4 to 4 do begin
   if A_TURN=1 then writeln (D,'A Psi[',i,']=',PSI_a[i]) else writeln (D,'B
Psi[',i,']=',PSI_b[i]);
  end;
  writeln(D);
  A_TURN:=A_TURN*-1;
 end;
 A_TURN:=1;
 writeln (A,'PSI_a=',S_a,' PSI_b=',S_b);
 for ALTERNATE:=1 to 2 do begin
  for RHP_e:=1 to RHP_i do begin
   writeln; writeln(A);
   if A_TURN=1 then write(A,'Actor A ') else write(A,'Actor B ');
   writeln(A,'RHP(ego) is ',RHP_e);
   writeln(A,'Vk structure is ',V);
   writeln(A,'Where Vk=',Vk,' Vr=',Vr,' tc=',tc);
   writeln(A,'and Dc=',Dc);
   for n:=endT downto 0 do begin
    write(A,'n=',n,' ');
    if n<10 then write(A,' ');
    for t:=1 to endT do begin
     if A_TURN=1 then write(A,ARIST_A[t,n,RHP_e]) else write(A,ARIST_B[t,n,RHP_e]);
    end;
    writeln(A);
   end;
   write(A,'     start');
   for t:= 0 to endT-10 do begin
    write(A,' ');
   end;
   writeln(A,'endT');
  end;              {end of the RHP_e loop}
```

```
  A_TURN:=A_TURN*-1;
 end;                 {end of the alternate loop}
end;

{*************************************************************************}
{* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *}
{ * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *  }
{* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *}
{ * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *  }
{*************************************************************************}

begin            {main program}
 FLUFF;          {fill in parameters & get user prompt}
 FILE_SETUP;     {open disk output files}
 for S_a:=1 to 5 do begin
  for S_b:=1 to 5 do begin
   READ_PSIs;    {get the specific strategies to be used this time}
   BACKWARDS;    {backwards iterate to solve for aristos, aka B*}
   FORWARDS;     {calculate expected fitness for aristos}
   PRNTARIS;     {pipe the aristos matrices out to disk}
  end;
 end;
 FILE_CLOSE;     {& put out the cat...}
end.
```