Strategically Developed Phenotypes and the Evolution of Signals

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Abstract

In the first part of this thesis, a general one dimensional theory of strategically determined phenotypes is developed and applied to biological signalling games. Abstract modular modelling techniques are utilised to solve hitherto analytically intractable problems including error-prone signalling, and how to incorporate genetic features into optimization models. Links are drawn between previous biological models, such as the War of Attrition and Strategic Handicap models. Mistakes in previous biological models are recognised and, where possible, rectified. A number of novel insights into biological phenomena arising from the models are presented, including analyses of: when free signals are possible; honest signalling of future paternal investment; dimorphic signals; the effects of the mechanisms of female discrimination in sexual selection on male signalling strategies; and the effects of relatedness on the magnitude and stability of equilibrium signalling strategies. It is argued that Zahavi's proposed demarcation between signal selection and natural selection is unjustifiable from a theoretical perspective.

The second part of the thesis concerns the epistatic handicap process of sexual selection. Unlike the conditional and revealing handicap mechanisms, the epistatic or 'Zahavian' handicap mechanism of sexual selection has hitherto found scant support in the theoretical literature, as it appeared to function only under the most extreme conditions. A continuous game theory model, a quantitative genetics model, and a three locus major gene model are presented which show that the epistatic handicap mechanism can function, independent of the Fisher process of sexual selection, under reasonable assumptions. Moreover, the game theory model illuminates the connection between the strategic and epistatic handicap mechanisms. The quantitative genetics and major gene models, together with a fourth model, are also used to show that a general argument concerning indirect genetic correlations, which has appeared in a number of papers on sexual selection, is specious.

Finally, a general theorem on games that satisfy the single-crossing condition (also known as the sorting, Spence-Mirrless, or constant sign condition) which underlies many of the results presented in the first part of the thesis is proven in appendix C. Applying a limit result to this general theorem provides a new proof of, and extensions to, Nash's existence result for equilibria to strategic-form games without having to resort to Kakutani's fixed point theorem.

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1 Introduction

1.1 Brief Historical Context

Since the publication of Zahavi's original paper proposing the handicap principle (Zahavi 1975), there has been a lively resurgence of theoretical interest in the possible mechanisms of sexual selection (Darwin 1859, 1871; see Andersson 1994 and Johnstone 1995 for extensive bibliographies). In particular, much of this interest has been focussed upon the evolution of exaggerated traits: traits that appear to be less than optimal for the functioning of the organism in its environment.

The proposal that exaggerated traits act as indicators of some underlying quality has been recurrent in the literature. It is rarely recognized that even Darwin hypothesized it, albeit in a rather exasperated manner, as an explanation of the often vivid colouration of nudibranchs:

> Nor is it at all obvious how the offspring from the more beautiful pairs of hermaphrodites would have any advantage, so as to increase in numbers, over the offspring of the less beautiful, unless indeed vigour and beauty generally coincided. (Darwin 1871, Volume 1, p327)

Wallace (1889), on the other hand, saw such exaggerated traits as by-products of traits that were 'fit' Colour was, in Wallace's view, a natural property of biological tissue; exaggerated ornaments were the direct outcome of superabundant health and vigour. The indication of health and vigour was a significant part of Fisher's conception of the exaggeration of traits by sexual selection (Fisher 1915, 1930), and was stressed in William's (1966) rendering of sexual selection.

In spite of this, Zahavi's handicap principle (Zahavi 1975, 1977a) encountered much initial scepticism (e.g. Maynard-Smith 1976, 1978a; Davis & O'Donald 1976, Kirkpatrick 1986). With the appearance of more favourable models (e.g. Nur & Hasson 1984; Andersson 1986a,b; Pomiankowski 1987, 1988), opinion of the handicap principle progressed from this initial skepsis to qualified acceptance (Maynard-Smith 1987) through to its current status, regarded as a plausible description for the evolution of exaggerated sexual ornaments (e.g. Grafen 1990a,b; Iwasa et al. 1991; and reviews in Andersson 1994; Møller 1994).

Subsequently, Zahavi proposed that the handicap principle has broader implications than those outlined in his first papers. He has proposed that Darwin's natural versus sexual selection dichotomy is a misdemarcation, natural versus signal selection being the correct distinction (Zahavi 1981, 1987, 1991). In particular, he suggested that signals, a term in which he included much which had hitherto been referred to as sexually selected traits, must be differentially costly to individuals to be evolutionarily stable. He further hypothesized (Zahavi 1977b) that much of what appeared to be altruism was, in fact, costly handicap signalling in disguise. There is now a plethora of models applying the handicap principle to signalling contexts other than sexual selection (Godfray 1991; Vega Redondo & Hasson 1993; Yachi 1995; Adams & Mesterton-Gibbons 1995).

It is debatable whether what is now regarded as the handicap principle is identical with Zahavi's original delineation. Indeed, Maynard-Smith (1985, 1987, 1991) has distinguished three categories of handicap mechanisms: epistatic (or Zahavian) handicaps, revealing handicaps, and conditional handicaps. All subsequent discussions of the handicap principle have been based on this classification scheme. However, it is not clear that these categories are distinct, or even well defined (Collins 1993), and different authors have used these labels in different ways.

1.2 What this Paper is About

This paper (chapters 1 to 8) systematically investigates the evolution of strategic signals via an optimization theory approach (Maynard-Smith 1978b). The analysis is, in the main, concerned with the existence of evolutionarily stable strategies (Maynard-Smith 1982) and not with whether the particular ESS is reachable from another state via a series of mutations, though some discussion is given of these points (see sections 2.2.10 and 9.8).

1.2.1 A Rough Definition of Strategic Signals

Strategic signals are defined roughly as follows:

> At equilibrium, a strategic signal maximizes the *relative* fitness of individuals of each quality by being phenotypically sensitive; i.e. the level of the signal expressed in a given phenotype is determined in such a manner that, given the level of signal expressed in other phenotypes, the level of signal expressed in the given phenotype maximizes the expected relative fitness of that phenotype (cf. Parker 1982).

The term 'strategic signal' can be used almost interchangably with Grafen's notion of a 'strategic handicap' (Grafen 1990a,b). In fact, Grafen's (1990a) strategic handicap model turns out to be a special case of the mathematical results that are presented later in this paper (see sections 2.3 and 6.2).

The significant difference between Grafen's notion of a strategic handicap, and the results presented here, relates to the necessity of cost in signalling. There are a number of results in the literature that show that the necessity of cost in signalling is theoretically untenable (Enquist 1985; Maynard-Smith 1994; Hurd 1995). Even in non-coordination (i.e. conflict) signalling situations, free or cheap signals can be evolutionarily stable. The epithet 'handicap' evokes a sense of costliness, and the results presented later show that this is not a necessary aspect of a strategic evolutionarily stable equilibrium. It is for this reason that I refer to 'strategic signals', as opposed to 'strategic handicap signals'

1.2.2 Why Focus on Strategic Signals?

If strategic signals are just a refinement of the strategic handicap principle, and there are so many other handicap mechanisms, and at least one other major theory of sexual selection (the Fisher process), why focus on strategic signals?

The answer to this question is that strategic signals are fundamental to the theory of signal/sexual selection because they are maximally phenotypically sensitive. To see why this is important, consider the following:

- In the case of pure epistatic handicaps (Pomiankowski 1988; Iwasa et al. 1991) or pure Fisherian traits (e.g. O'Donald 1980, 1973, 1967, 1962; Lande 1981; Kirkpatrick 1982; Pomiankowski et al. 1991) the exaggerated traits are, by definition, unaffected in their development by an individual's quality. Quality is not considered in the models of the Fisher process cited above (though it was an important aspect of Fisher's argument) and only becomes important in the epistatic handicap theory when the ability to bear an ornament is considered, e.g. effect on survival. This is, in general, an unstable condition in the context of selection. Individuals of different qualities will have different 'balance points' at which the cost of further exaggeration of the trait outweighs the benefit to be obtained by increasing their success in signalling contests. Modifiers that fine-tune the level of development of the trait by an individual's ability to bear it would be able to spread. Neglecting constraints on the genetic system involved, the only circumstances in which a modifier could not invade is when there is no phenotype which could not increase its fitness by producing a different level of signal, i.e. at a strategic signalling equilibrium.
- Revealing handicaps are evolutionarily stable because 'high' signals cannot be faked by 'low' quality individuals. There are two reasons why this may be so:

  First, they may not be able to be faked because altering the development of the trait (e.g. extending period of development or expending extra resources) may be more costly than any benefit that can be obtained, i.e. modifiers are detrimental. As pointed out by Collins (1993) this renders the revealing handicap indistinguishable from the strategic handicap.

  Second, the required variation may not arise. Although this may be empirically true, this is akin to saying signals are honest and evolutionarily stable simply because they are; a theoretical investigation cannot add anything further. It has been argued that apparently cheap behavioural signals cannot be stable because cheats can subvert the signalling system without incurring cost (Andersson 1980; though see Enquist et al. 1985; Popp 1987; Waas 1991). Consistency demands that if we assume that behavioural cheats can and do arise with enough regularity to make such systems evolutionarily unstable, then, *ceteris paribus*, we should assume the same about other traits. Succinctly, this type of revealing handicap could be the actual norm, but there is little room for theoretical analysis and it clashes with a common theoretical assumption (though see Hasson 1989, 1990, 1991). Similar comments apply to conditional handicap models in which it is assumed that individuals of a low quality must exhibit the handicap trait at a lower level than individuals of high quality (e.g. Maynard- Smith 1987, Table 1, model (c)).

This perspective might best be summarised by translating its conclusions into the language of 'adaptive topographies' or 'fitness landscapes' (Wright 1931, 1932): only strategic signalling equilibria are at peaks of the relevant fitness landscapes. Other equilibria are, at best, only approximations to the peak—modifiers that are higher up the fitness hill, that push the system closer to a strategic equilibrium, can always invade.

1.3 Criticisms of the Approach

The optimization approach to evolution has been criticized from at least three perspectives.

1.3.1 Adaptationism is Not Holistic Enough

The first criticism originates with the critique of the adaptationist programme by Gould & Lewontin (1978). The basic criticism is that 'adaptationists' naïvely break organisms into unitary traits and place too much emphasis on functional explanations of these traits, missing the more interesting and important points: constraints due to phyletic heritage, ontogeny, and general architecture.

Jamieson (1986) has also criticised the functional approach to studying behaviour from a similar perspective, pointing out that it assumes natural selection as an axiom. He argues that although predictions derived from selection theory are empirically supported in general, these predictions are not peculiar to the selection process, and determining which of the multifarous plausible processes has lead to the establishment of a particular trait is not easily discernable from simple observations.

A full rebuttal of these criticisms is not possible in the space available here. Admittedly, evolutionary ecology and life history analysis are very much focussed on functional questions, disregarding the other three of Tinbergen's (1963) four facets of ethology. One cannot deny that any complete explanantion of an aspect of an organism must make reference to its phylogeny, ontongeny, and the mechanism by which it operates. However, despite its failings, it would be misguided to deny the successes of the functional approach; sex ratio theory is perhaps the premier example (reviewed in Charnov 1982; see Charnov 1993 for a more recent bibliography). The optimization approach is best seen as an endeavour to understand the diversity of life; it is definitely not an attempt to demonstrate that organisms are perfectly adapted (see Maynard-Smith 1978b; Parker & Maynard-Smith 1990).

It should be added here that the traits in question in this paper are assumed to exist in the population, at least in some sense. The central question under consideration is not how the trait has arisen in the population but given that a trait exists or can exist, what is the evolutionary stable intensity of its expression?

1.3.2 Underlying Genetic Structures Cannot Support Phenotypic Optimization Models

The second kind of criticism of the optimization theory approach arises from the observation that population distributions of phenotypes must be supportable by the underlying genetic system. The simplest criticism of this type arises from heterozygotic advantage. A game theory model may predict that a certain state is optimal and that the evolutionarily stable state is for all individuals in the population to be in this state, but the underlying genetic system may only be able to acheive this state by a heterozygotic solution; in a sexual population recombination ensures that not all individuals can be heterozygotes. An excellent example of this is sickle cell anaemia which has evolved and developed significant expression in human populations numerous times (Harrison et al. 1988). In areas in which there is a high incidence of malaria, the optimal genotype for an individual seems to be the heterozygotic one.

The problem of pleiotropy is related to this. A trait may be acheivable but, because of genetic pleiotropy or developmental correlation, acheivement of the trait predicted may be at the expense of altering an important second trait. Both this problem and the problem of heterozygosity can be avoided by ad hoc alterations of the assumptions in the optimization model. There is, however, a more critical problem.

Whilst Wright's notion of a fitness landscape makes sense for single traits controlled by single haploid or diploid genetic systems (Kingman 1961), problems occur when there are two or more loci in a genetic model. In general, the fitness of a population due to a trait controlled by two or more loci, given an initial distribution of alleles, does not increase from generation to generation (Moran 1964; Karlin 1975; Karlin & Carmelli 1975). This is a direct contradiction of Fisher's Fundamental Theorem of Natural Selection (Fisher 1930) (see also Weibull 1995, p109).

The problems outlined above all rely on genetic constraints preventing the optimal strategy or strategies from being expressed. Recently, a number of authors have suggested a solution to this problem (Hammerstein & Selten 1994; Eshel 1996; Hammerstein 1996; Matessi & Di Pasquale 1996; Weissing 1996). If a long term perspective is taken then the evolutionary removal of the above constraints should be taken into account, e.g. by the addition of new loci that affect the trait. Although for fixed sets of loci and associated alleles, Fisher's Fundamental Theorem is not true in general, the optimization concept of a phenotypic ESS provides a necessary condition for evolutionary stability in the less restrictive long term perspective. Genetic models, therefore, address issues of short term evolution—the immediate effects of selection on a polymorphic population. Optimization equilibrium concepts are more suited to the analysis of the evolution of traits over longer periods of time.

The demarcation between long and short term evolution is not well defined. It is quite likely that the distinction may differ between traits (cf. Edinger's Hypothesis which states that during evolution, body and leg size change first, then teeth, then brain size and morphology (Geist 1974, and refs. therein)). It is plausible that in some cases the length of time is much shorter than the lifetime of a species, and in others, significantly longer. That is, some traits may never reach a long term equilibrium. Moreover, there are some traits that are likely to be in a constant state of flux due to aggressive coevolution of other species (Van Valen 1973), e.g. the immune system of one species due to the coevolution of parasites (Hamilton & Zuk 1982). The theoretical results derived by Hammerstein et al. require that the equilibrium that is obtained is genetically monomorphic, or at least functionally monomorphic, and there appear to be good reasons (Weissing 1996) to suspect that their new approach cannot deal effectively with polymorphic equilibria.

In chapter 3 some methods are outlined for handling the assumption that there is additive genetic variance in the traits that are being signalled and the traits that are being optimized. Although, the approach taken is not ideal, and cannot answer the serious questions arising from genetic constraints that have been raised here, it makes weaker assumptions than those made in standard quantitative genetics approaches (e.g. Pomiankowski et al. 1991; Iwasa et al. 1991).

1.3.3 ESSs May Not Be Reachable, and What is Reachable May Not be an ESS

The final criticism of the approach taken here, although based on genetic intuitions, comes from optimization theory itself. It is in fact two separate, but in a sense complementary, criticisms. First, the ESS condition does not guarantee that natural selection should favour a mutation in a population fixed on a strategy near to an ESS which is in the direction of the ESS (Eshel & Motro 1981; Eshel 1982, 1996).

In light of this observation, Eshel & Motro (1981) have provided the notion of a continuously stable strategy (CSS). A CSS is, basically, an ESS such that if the population strategy is fixed on a value close enough, mutations which give rise to a strategy closer to the ESS strategy are selected for and those which render an individual's strategy further away sustain a selective disadvantage. (This condition on the attraction of an ESS has been called m-stability (Taylor 1989) or convergence stability (Christiansen 1991). See Matessi & Di Pasquale (1996) for an attempt to generalize the notion of a CSS).

The converse problem is that there are circumstances in which there are strategies which are convergently stable, but are not themselves ESSs (Taylor 1989; Christiansen 1991). That is, the convergently stable value cannot be maintained as a monomorphic equilibrium. It appears (Eshel 1996 quoting unpublished results of Eshel & Motro) that in this case, selection will stabilize upon a small variance distribution around the convergence stable value.

As stated in section 1.2 the approach taken here is almost exclusively an analysis of the ESSs. However, some of these issues are discussed, where it is appropriate in the text, in relation to the ESS results obtained.

1.4 The Modular Approach

The terms used in the results that follow are perforce abstract, and the proofs are somewhat more arduous and mathematically sophisticated than is usual for biological signalling models. Abstraction in this case should not, however, be confused with impractical complexity. In fact, by being more abstract the results presented here are closer to the logic of the arguments used by biologists. This abstractness has allowed a single treatment to encompass models of sexual selection, predator prey signalling etc. whilst dealing with both error-prone and error-free signals.

Obtaining abstract results is an inversion of the philosophy of modelling that has previously prevailed in the application of game theoretic optimization models in biology. Rather, it has been typical to outline specific assumptions about the nature of the contest, the number of contestants etc. and then argue that deviating from these assumptions will not qualitatively affect the result. In this paper, the general result is proven, and it is then shown how specific cases satisfy the conditions of the general result.

A significant aspect of the theorems presented here is that they are modular. Treatments of sexual selection and signals are, by the nature of the subject, fragmented. Assumptions are made about both the signaller's and receiver's behaviours, the nature of the benefits that they receive by signalling and attending to signals, and the types of costs that these behaviours incur. By being both extremely general and modular, the theorems allow assumptions to be 'mixed and matched'

The power of this abstract modular philosophy is highlighted by the following two examples:

1. The strategic handicap model due to Grafen (1990a), turns out to be a special case of Proposition 2.3. Interestingly, Grafen arrived at his model via population genetic arguments. The models presented here were developed as ESS game theory results. This should not be surprising, considering that the ESS concept was developed as the limit of a population genetic argument (Maynard-Smith & Price 1973; Maynard-Smith 1982). Grafen's model made many specific assumptions, including:
    (a) All females are identical.
    (b) Females only mate once.
    (c) Unmated females encounter individual males at random with respect to genotype and quality in a homogeneous Poisson process. If they reject a male, they may not return to him if they don't find a better male.
    (d) A female's reproductive effort is not affected by the perceived quality of their mate.
    (e) Female strategies 'know' the distribution of males and the expected level of signalling.
    (f) There is no error in the signals themselves, nor in their receipt.
    (g) The male population distribution before accounting for the effects upon survivorship, is independent of the population signalling strategy.
    (h) Differential survival is only assumed prior to the mating season.

    But the solution to Grafen's model is so specific that conclusions about the effects of assumptions that differ from the above cannot be drawn with certainty. The modular treatment given here allows these assumptions to be broken, individually or together, and shows their effects upon the signalling equilibria. In a companion paper, Grafen (1990b) attempted to develop a very general and abstract ESS result which did not make such specific assumptions, but this fell short of being able to encompass his population genetics model and, because it did not partition an individual's total fitness, made it difficult to work with.

2. Grafen & Johnstone (1993; Johnstone 1994, 1996) have considered models of error-prone strategic handicap signals, but only been able to provide

computational solutions. From these computational results they drew several conclusions. The modular analytical model provided here, highlights the major problem of the computational approach: the results are specific to the functions and parameters used in the simulation. Although this problem can be mitigated by choosing a wide range of parameters, this presupposes that it is appreciated which parameters are important and what a wide range of parameters is. This is not always obvious without at least some mathematical analysis, and in this case it turns out that some of the results that they obtained are misleading, due to the form of the cost function that was chosen (see section 6.4). The results obtained below do not assume specific costs, but assume minimal conditions that must be satisfied by the cost function, and thus highlight an important class of ESSs that were missed by the computational analysis.

1.5 Basic Description of the Model

1.5.1 Structure of the Model

As outlined above, the approach taken here is modular. The fitness of a signaller is partitioned into components and conditions are derived which, if satisfied by the relevant components, allows conclusions to be drawn about the existence and nature of the evolutionary stable strategies (generically referred to as ESSs).

Two types of partition are considered. The first is additive, that is:

$$\text{Expected Fitness} = \text{Expected Benefit} - \text{Expected Cost}$$

This is the structure of the payoffs of many game theory models in the literature (e.g. The Hawk- Dove Game (Maynard-Smith and Price 1973; Maynard-Smith 1982), The War of Attrition (Maynard- Smith 1974), The Opponent Independent Cost Game (Parker 1979, 1983a), and some strategic handicap models (Grafen & Johnstone 1993; Johnstone 1994)). In mathematical notation, an individual's fitness may then be written:

$$P(A, a, q) = V(A, a, q)N(A, a) - C(A, a, q) \tag{1.1}$$

where a represents the individual's level of signal or exaggeration of trait, q the individual's quality, and $A(q)$ the population's signalling strategy. It is assumed that a ranges over a connected set of real numbers, $\mathcal{A}$, and q over a compact interval of real numbers, $\mathcal{Q}$. Expected Cost is represented by C. Expected Benefit is further partitioned into the expected value of the resource contested, V, and the expected amount of, or probability of obtaining, the resource, denoted by N. It is assumed that the success of signalling is independent of an individual's quality, being entirely due to the level of signal or exaggerated trait borne. Thus, N is assumed not to be a function of q.

The second type of partition considered is inspired by a simple decomposition of an individual's fitness in the context of sexual selection:

$$\begin{aligned}\text{Expected Fitness} = {} & \text{Expected Offspring Quality} \\ & \qquad\qquad\times \\ & \text{Expected Mating Success}\end{aligned}$$

×

Expected Survival

In mathematical notation:

$$P(A, a, q) = V(A, a, q)N(A, a)S(A, a, q) \tag{1.2}$$

Similar partitions of fitness have been used in strategic handicap models by Andersson (1982) and Grafen (1990a). V, N, C, and S are, of course, open to interpretations other than those that inspired them. Examples are given in chapter 8. Although the results in this paper are only derived for these two partitions, the actual scope of the results is much wider (see comment 2 in section 2.2.9 and comment 1 in section 2.3.5.), and they may be applied to circumstances other than signalling and sexual selection (see section 2.3.6 and chapter 8).

1.5.2 Techniques of Solution

Two techniques are used to investigate the existence and nature of ESSs to the models defined by equations (1.1) and (1.2). The first technique is to use a combination of differential equations and fixed point theorems. Differential equations have been used to analyse the strategic handicap principle previously (Andersson 1982; Grafen 1990b; Godfray 1991; Johnstone 1995), and in a sense they are the natural tool to use. However, they are not well suited to dealing with circumstances in which feedback from the global strategy, A, influences the local strategies, $A(q)$. Grafen (1990a) solved this problem by the application of a fixed point theorem. His approach has inspired the method used here, and it is shown in section 6.2.1 that the result of his model is a special case of the results derived in section 2.3.

The differential equation approach, however, requires assumptions that are not satisfied by, *inter alia*, models which incorporate error in signalling or the psychophysical response of receivers to the intensity of signals. The second technique used is based purely on the application of a fixed point theorem, being reminiscent of the approach taken by Nash (1950) for discrete games. Although, in some cases, this approach gives less information about the nature of the ESSs than that obtained by the differential equation approach, it more than compensates by providing existence results in situations that have hitherto seemed intractable to mathematical analysis. In particular, the case of error-prone signals, which have so far only been investigated by computation (Grafen & Johnstone 1993; Johnstone 1994, 1996). As stated in section 6.4, the analytical results have shown that some of the computational results are misleading. Further, this technique shows that some of the assumptions necessary for the differential equation approach eradicate a whole class of ESSs that are of potential biological significance.

1.6 Mathematical Requirements and Notation

Simple and general results have been obtained in this paper. Unfortunately, this has required a slightly more technical and significantly lengthier analysis than is usual in biological models. Mathematically, all that is assumed is a working knowledge of multivariate differentiation (Fleming 1977), measure theory in one dimension (Riesz & Nagy 1955) and the most basic facts about continuous maps and compactness (Munkres 1975).

It has proven impossible to retain a completely consistent as well as suggestive notation. Some ubiquitous symbols and their usual meanings are listed in Table 1. Generally:

Notation	Usual Meaning
P	expected individual fitness or payoff
V	expected value of contested resource
N	expected amount of resource obtained
C	expected cost of advertising
S	expected chance of survival
K	cost of discrimination to receivers
A	population advertising strategy
A^*	ESS advertising strategy
D	population receiver strategy
D^*	ESS receiver strategy
R	reproductive value
f	signaller quality population density
F	cumulative distribution of signaller quality
f°	receiver quality population density
F°	cumulative distribution of receiver quality
q	individual quality
a	individual advertising level
$\mathcal{Q}$	set of possible qualities
$\mathcal{A}$	set of possible advertising levels
$\mathcal{D}$	set of possible receiver strategies
$\mathcal{S}$	set of plausible signalling strategies
$M(A)$	the 'best response to A'; functional from $\mathcal{S} \to \mathcal{S}$
$\Lambda(n)$	see section 5.1.3 for definition
$\aleph_0$	countable infinity
$L(\mathcal{Q})$	set of all functions Lebesgue integrable on $\mathcal{Q}$
$\mathcal{L}(\mathcal{Q})$	Banach space of all functions Lebesgue integrable on $\mathcal{Q}$
$E(X, x)$	expectation value of x given X

Table 1: *Definitions of ubiquitous and important notation.*

- **Lower case letters** represent variables. Distinguishable but similar variables are often separated by subscripts or the accent, $'$ The subscripts 'max' and 'min' represent the maximum and minimum values that a variable may take.

- **Upper case letters** represent functions. Distinguishable but similar functions are often separated by sub- or superscripts. However, the accent, $'$, represents the derivative of a function of one variable, and numeric subscripts represent partial derivatives. For example, $P_{23}(A, a, q)$ represents the following second order partial derivative of the functional P:

$$\frac{\partial}{\partial q}\left(\frac{\partial P}{\partial a}\right)$$

Order is important, as P_{23} does not necessarily equal P_{32} (in fact there are examples in which P_{23} exists everywhere, but P_{32} does not exist anywhere!), although this is generally true almost everywhere for reasonable functions.

Upper case calligraphic letters represent sets or topological spaces.

Lower case Greek letters tend to represent small quantities, variables, or parameters.

Upper case Greek letters represent functions.

An upside down, 'A', i.e. $\forall$, represents the phrase 'for all' The terms 'almost everywhere' and 'almost always', usually abbreviated to 'a.e.' and 'a.a.' respectively, are used in a technical sense (Fleming 1977, p231). The terms 'increasing' and 'strictly increasing' are also used in their technical sense; a function $f(x)$ is increasing in x if $x_2 > x_1$ implies that $g(x_2) \geq g(x_1)$, whilst g is strictly increasing if and only if $g(x_2) > g(x_1)$.

Square brackets represent closed ends of intervals and open brackets represent open ends of intervals, thus $[0, 1)$ is the set of real numbers containing all the numbers that are greater than 0 and less than 1, including 0 but not including 1. In some places in the text, intervals like $[0, \infty]$ appear; this represents the one point compactification of the subset of real numbers $[0, \infty)$ (see Munkres 1975); $F(\infty)$ represents $\lim_{q\to\infty} F(q)$, if it exists.

Continuity and differentiability of functions are defined relative to the set on which the functions are defined. For example, the statement '$A(q)$ is differentiable on $[q_{\mathrm{min}}, q_{\mathrm{max}}]$' should be understood to mean '$A(q)$ is differentiable on $(q_{\mathrm{min}}, q_{\mathrm{max}})$, differentiable from the right at q_{min} and differentiable from the left at q_{max}'

One sided limits are often used in the following. The limit of a funciton $f(x)$ as x approaches x' from the left is represented by:

$$\lim_{x\uparrow x'} f(x)$$

Limits from the right and two-sided limits are represented in a similarly, but with '$\uparrow$' replaced by '$\downarrow$' or '$\rightarrow$' respectively.

1.7 Equilibrium Conditions

The application of game theory to biology is facilitated by the existence of a natural solution concept, the ESS of Maynard-Smith & Price (1973). Verbally, an ESS is a strategy which no mutant strategy can invade. This statement, however, has more than one possible mathematical interpretation; the 'correct' formulation is context dependent (see Weibull (1995) and Eshel (1996) for summaries and discussion of current evolutionary stability concepts).

The following is a very general set of criteria for a strategy, S, to be an ESS (cf. Hammerstein's suggestion in Maynard-Smith 1982, p24): Let the payoff to an individual playing a strategy A, in a population playing B, be represented by

---

$P(B, A)$, and let $\mathcal{S}$ denote the set of all possible strategies. S is an ESS if for all $S' \in \mathcal{S} - \{S\}$ either it satisfies the **first order condition**:

$$P(S, S) > P(S, S')$$

or if $P(S, S) = P(S, S')$ it satisfies the **second order condition**: there exists $\delta' > 0$ so that for all $0 < \delta \leq \delta'$:

$$P(\delta S' + (1 - \delta)S, S) > P(\delta S' + (1 - \delta)S, S')$$

where $\delta S' + (1 - \delta)S$ represents a population of individuals, a proportion δ of which play S', and $(1 - \delta)$ play S. Note that an ESS is relative to the set of possible strategies, $\mathcal{S}$.

If P is continuous in the population mix of strategies, then the second order condition outlined above implies the first order condition, and thus the first order condition is superfluous. In the case of two player games with payoffs that are linear in the population strategy, the above definition is equivalent to the original definition of Maynard-Smith & Price (1973) (see Taylor & Jonker 1978). If linearity or continuity is not satisfied, then the original definition of an ESS is not necessarily appropriate. It should also be noted that the definition of an ESS only considers invasion by a single mutant strategy. ESSs need not be robust to simultaneous invasion by a number of strategies (for examples see Binmore 1997).

In complex and abstract models, a problem of practicality arises with this definition; checking the second order condition requires a more specific knowledge of the underlying structure of the game than does checking the first order condition. It has proven useful to use four first order concepts in the sequel. These are:

PBR A strategy $A^*(q)$ is said to be a pointwise best response (PBR) to a strategy A if for all $a \in \mathcal{A}$ and all $q \in \mathcal{Q}$:

$$P(A, A^*(q), q) \geq P(A, a, q)$$

PNE A strategy $A^*(q)$ is said to be a pointwise Nash equilibrium (PNE) if for all $a \in \mathcal{A}$ and all $q \in \mathcal{Q}$:

$$P(A^*, A^*(q), q) \geq P(A^*, a, q)$$

That is, A^* is a PNE if and only if it is a PBR to itself.

SNE A strategy $A^*(q)$ is said to be a summed Nash equilibrium (SNE) if for all possible strategies, $A(q)$, such that $\int_{\mathcal{Q}} \mid A^*(q) - A(q) \mid f(q) \cdot dq \neq 0$:

$$\int_{\mathcal{Q}} (P(A^*, A^*(q), q) - P(A^*, A(q), q)) f(q) \cdot dq \geq 0$$

ESS A strategy $A^*(q)$ is said to be an ESS if for all possible strategies, $A(q)$, such that $\int_{\mathcal{Q}} \mid A^*(q) - A(q) \mid f(q) \cdot dq \neq 0$:

$$\int_{\mathcal{Q}} (P(A^*, A^*(q), q) - P(A^*, A(q), q)) f(q) \cdot dq > 0$$

Thus, both SNEs and ESSs are not unique functions, but sets of functions that differ only on a set of measure zero. For a strategy to be uninvasible, it must be an SNE (cf. Grafen 1990a), but this condition is not sufficient (e.g. Parker 1979). However, the use of a strict inequality in the definition of an ESS is too stringent in general; neither the 'ESS' to the symmetric War of Attrition (Maynard-Smith 1974) nor a mixed 'ESS' to the Hawk-Dove Game (Maynard-Smith 1982) satisfies the condition that is referred to as an ESS here. On the other hand, the usual definition of an ESS is only sufficient if the population in question is infinite (Riley 1979b, 1980). In this paper these issues are sidestepped, as it turns out that every strategy that is an SNE in this paper is also an ESS and thus, second order conditions do not need to be considered.

It should be noted that in the definition of SNEs and ESSs, integrability conditions implicitly imply that the set of strategies against which A^* is compared is restricted to those for which the integrals exist; there is the possibility of two strategies being incommensurable. This is not a serious problem as, in general, all biologically reasonable functions (e.g. piecewise differentiable or piecewise monotonic functions) will be comparable.

One of the methods regularly employed in this paper to analyse complex signalling games, is to break them down into simple subgames which are easier to solve. *Prima facie*, the problem with this approach is that is does not allow for interaction between the subgames. The solution is to solve each subgame for a wide class of external conditions (i.e. conditions possible due to strategies played in the other subgames), and then show that there are mutually compatible sets of strategies for the subgames.

Sexual selection due to female discrimination provides a clear example of this. The optimal male signalling strategy, and hence the equilibrium male population strategy is, in part, determined by the female population's discrimination strategy. Conversely, the optimal female discrimination strategy, and hence the equilibrium female population strategy is, in part, determined by the male population's signalling strategy.

Mathematically, if $P_M(D_{pop}, A_{pop}, A_{ind})$ and $P_F(A_{pop}, D_{pop}, D_{ind})$ represent the fitnesses of individual males and females respectively, given the population signalling (A_{pop}) and discrimination (D_{pop}) strategies, then a strategy which is an equilibrium to the complete game is one which satisfies:

$$\begin{aligned} P_M(D^*, A^*, A^*) &\;\rhd\; P_M(D^*, A^*, A), && \text{for all } A \neq A^* \\ P_F(A^*, D^*, D^*) &\;\rhd\; P_F(A^*, D^*, D), && \text{for all } D \neq D^* \end{aligned}$$

where $\rhd$ represents the inequality relevant to the equilibrium condition under consideration. This approach is returned to in some detail in chapter 3, and example calculations are given in chapter 5.

2 Strategically Developed Signals

2.1 Introduction

Signalling strategies are the main focus of this chapter. In general, receiver strategies are assumed without justification. The interaction between signaller and receiver strategies is held in abeyance until chapters 3 and 5. This may seem unusual, as the existence of a signalling equilibrium in previous models has often been critically dependent upon the interaction between receiver and signaller behaviour or receiver costs (e.g. Kirkpatrick 1985; Dawkins & Guilford 1991). However, it turns out that the inclusion of receivers trying to optimize their fitness has very little effect on the qualitative results obtained here. In any case, the models solved in this chapter are valid without modification for passive attraction models of sexual selection (cf. Levin 1985; Arak 1988).

2.2 D.E. Approach to Additive Fitness Partitions

This section considers signalling games defined by additive fitness partitions. In particular, games in which V is independent of a are focussed upon, i.e. games defined by:

$$P(A,a,q) = V(A,q)N(A,a) - C(A,a,q) \tag{2.1}$$

This condition on V is considerably relxed in later sections.

The approach taken here is to derive basic facts about PNEs and ESSs of the above game, introducing conditions only as they become necessary (Lemmas 2.1 to 2.7) before proving the main result (Proposition 2.1). Doing this emphasizes which conditions are necessary for each particular aspect of the result. This work is similar to a number of games in the economics literature (e.g. Spence 1973, 1974; Riley 1979; Quinzii & Rochet 1985; Mailaith 1987).

2.2.1 ESSs are Increasing in Quality

Lemma 2.1 *Consider the game defined by equation (2.1). Assume that C is absolutely continuous in a. Further assume that F and C_2/V are absolutely continuous in q, and that:*

$$\frac{\partial}{\partial q}\left(\frac{C_2(A,a,q)}{V(A,q)}\right) < 0, \quad \text{for a.a. } (a,q) \in \mathcal{A} \times \mathcal{Q}. \tag{2.2}$$

then if A^* is a PBR of A then it is increasing in q. In particular, any PNE is increasing.

Proof: Suppose that there exists a PBR, A^*, of A that is not increasing, then there exists $q_1 < q_2$ for which $A^*(q_1) > A^*(q_2)$. As it is assumed that A^* is a PBR of A:

$$\begin{aligned} P(A,A^*(q_1),q_1) &\geq P(A,A^*(q_2),q_1) \\ P(A,A^*(q_2),q_2) &\geq P(A,A^*(q_1),q_2), \end{aligned}$$

which in turn implies that:

$$\frac{C(A,A^*(q_1),q_1)}{V(A,q_1)} - \frac{C(A,A^*(q_1),q_2)}{V(A,q_2)} + \frac{C(A,A^*(q_2),q_2)}{V(A,q_2)} - \frac{C(A,A^*(q_2),q_1)}{V(A,q_1)} \leq 0 \tag{2.3}$$

The inequality may be rewritten:

$$\int_{q_1}^{q_2}\int_{A^*(q_2)}^{A^*(q_1)} \frac{\partial^2}{\partial q \partial a}\left(\frac{C(A,a,q)}{V(A,q)}\right) \cdot da dq \geq 0.$$

This is impossible because of condition (2.2) and the fact that the integration is over a set of positive measure. If A is a PNE then it is a best reponse to itself and therefore increasing. □

Equation (2.2) may also be written, perhaps more enlightingly, in the form:

$$\frac{C_{23}(A,a,q)}{C_2(A,a,q)} < \frac{V_2(A,q)}{V(A,q)}$$

Note that $N(A,a)$ does not appear in equation (2.3) which implies that if a PNE exists it must always be increasing in the quality of the signaller, regardless of whether the receivers value high signals more than, or even as much as, low signals. Thus, Lemma 2.1 suggests that we should expect any reasonable receiver strategy to lead to N being an increasing function of signalling level observed.

2.2.2 Success Minus Relative Cost is Strictly Increasing and Continuous in Individual Quality

Lemma 2.2 *Under the conditions of Lemma 2.1, if* A^* *is a PBR of* A*, then* $P(A,A^*(q),q)/V(A,q) + C(A,a_{\min},q)/V(A,q)$ *is strictly increasing in* q*. Furthermore* $P(A,A^*(q),q)/V(A,q) + C(A,a_{\min},q)/V(A,q)$ *is continuous in* q*. In particular if* $C(A,a_{\min},q)/V(A,q)$ *is constant in* q*, then these results hold for* $P(A,A^*(q),q)/V(A,q)$.

Proof: The first result follows by contradiction. Suppose $q_1 < q_2$ that A^* is a PBR to A and:

$$\frac{P(A,A^*(q_1),q_1)}{V(A,q_1)} + \frac{C(A,a_{\min},q_1)}{V(A,q_1)} \geq \frac{P(A,A^*(q_2),q_2)}{V(A,q_2)} + \frac{C(A,a_{\min},q_2)}{V(A,q_2)} \qquad (2.4)$$

then note:

$$\begin{aligned}
\frac{P(A,A^*(q_1),q_2)}{V(A,q_2)} + \frac{C(A,a_{\min},q_2)}{V(A,q_2)} &= N(A,A^*(q_1)) - \frac{C(A,A^*(q_1),q_2) - C(A,a_{\min},q_2)}{V(A,q_2)} \\
&> N(A,A^*(q_1)) - \frac{C(A,A^*(q_1),q_1) - C(A,a_{\min},q_1)}{V(A,q_1)} \\
&\geq N(A,A^*(q_2)) - \frac{C(A,A^*(q_2),q_2) - C(A,a_{\min},q_2)}{V(A,q_2)}
\end{aligned}$$

where the last inequality is given by equation (2.4). By comparing the integrals of C_2/V with respect to a for q_1 and q_2, it is clear that this contradicts the assumption that A^* is a PBR to A.

Suppose that $P(A,A^*(q),q)/V(A,q) + C(A,a_{\min},q)/V(A,q)$ is not continuous, then there exists a point q' at which $P(A,A^*(q),q)/V(A,q) + C(A,a_{\min},q)/V(A,q)$ is either discontinuous from the right or discontinuous from the left. Without loss of generality, assume the latter, that is:

$$\lim_{q \uparrow q'} \frac{P(A,A^*(q),q) + C(A,a_{\min},q)}{V(A,q)} < \frac{P(A,A^*(q'),q') + C(A,a_{\min},q')}{V(A,q')}$$

Continuity of C_2/V then implies that there exists an interval (q'',q') so that for all $q \in (q'',q')$:

$$V(q)N(A,A^*(q')) - C(A,A^*(q'),q) > V(q)N(A,A^*(q)) - C(A,A^*(q),q)$$

which contradicts the assumption that A^* is a PBR.

The results for when $C(A, a_{\min}, q)/V(A, q)$ is constant in q follow trivially. □

2.2.3 Assumptions on N

The rest of the results in sections 2.2-2.3 depend upon properties of N. Consider the following conditions, under the assumptions A increasing (cf. Lemma 2.1), and $F(A, q)$ absolutely continuous and strictly increasing.

1. Suppose $a' \notin A(Q)$. $N(A, a') = \lim_{a \uparrow a_{\inf}} N(A, a)$, where $a_{\inf} = \inf\{a; a \in [a_{\min}, \infty]$ and $(a, a'] \cap A(Q) = \emptyset\}$; unless $A^{-1}(a_{\inf})$ is an interval, in which case no assumption is made. If $a_{\inf}$ does not exist then $N(A, a') = N(A, \inf A(Q))$. (This tells us how to interpret strategies not seen in the population. Basically, an individual is interpreted as being of the highest level normally seen in the population lower than the level at which it is signalling. See Fig.1 for further details of the intuition behind this condition.)

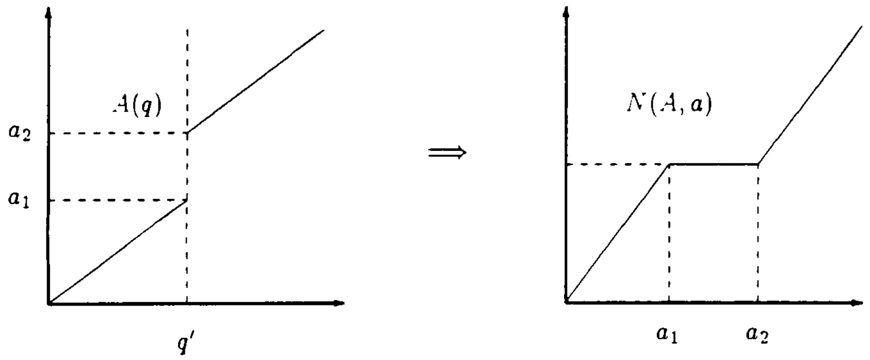

Figure 1: *Illustration of the intuition behind $N \in \mathcal{N}(1)$. Roughly, signals which are not normally seen in the population are treated as the nearest lower signalling level that is seen in the population, unless that level is signalled by a set of qualities of measure greater than zero. If an individual signals below $A(q_{\min})$ it is assumed that it is treated as if it signalled at $a_{\min}$. Note that $N \in \mathcal{N}(1)$ does not preclude N being discontinuous at a_2. However, continuity of N over signalling levels that aren't subscribed to in the population must be the case if $N \in \mathcal{N}(2)$. Condition $\mathcal{N}(1)$ has been chosen as it is satisfied by the War of Attrition (Maynard-Smith 1974), and the Opponent Independent Costs Game (Parker 1979). See section 6.1 for further details.*

2. Define $\#(a) \overset{\text{def}}{=} \text{card}\{q; A(q) = a\}$. N is continuous in a for all $a \in \text{int}\{a; \#(a) \leq 1\}$ (where 'int' denotes the interior of the set) and is left or right continuous (whichever is relevant) for $a \in \{a; \#(a) \leq 1\} - \text{int}\{a; \#(a) \leq 1\}$.

3. If A is strictly increasing on (q_1, q_2) then $N(A, a)$ is strictly increasing for all $a \in A((q_1, q_2))$. Note that this condition makes no claims about the

value of $N(A,a)$ if $a \in [A(q_1), A(q_2)]$ but there does not exist $q \in [q_1, q_2]$ for which $a = A(q)$.

4. If $\#(a') > 1$ (i.e. $A^{-1}(a')$ is an interval) then there exists $\epsilon > 0$ so that for all $a > a'$, $N(A,a) > N(A,a') + \epsilon$. (Let $Q_{a'} \overset{\text{def}}{=} \{q; A(q) = a'\}$. (See Fig.2 for further explanation of the motivation behind this condition.)
5. If $\#(a') > 1$ then there exists $\epsilon > 0$ so that for all $a < a'$, $N(A,a) + \epsilon < N(A,a')$. (See Fig.2 for further explanation of the motivation behind this condition.)

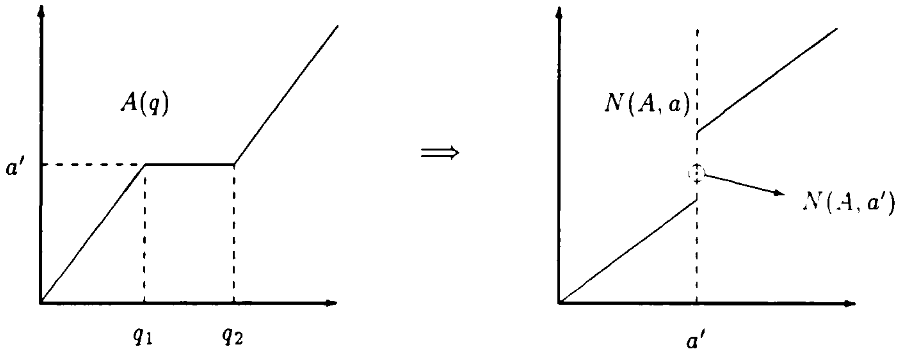

Figure 2: *Illustration of the intuition behind $N \in \mathcal{N}(4)$ and $N \in \mathcal{N}(5)$. If $N \in N(4)$ and $A(q) = a'$ for all $q \in [q_1, q_2]$ (left diagram) then $N(A, a)$ is discontinuous from the right at a' (right diagram). This is assumed to take into account the fact that receivers cannot separate qualities q_1 to q_2 which would lead to signallers of quality q_2 receiving less than they would at a separating equilibrium. Similarly, signallers of quality q_1 would be expected to receive more than they would expect at a separating equilibrium, and this is what $N \in \mathcal{N}(5)$ describes.*

6. If A_1 and A_2 are strictly increasing on (q_1, q_2) then $N(A_1, A_1(q)) = N(A_2, A_2(q))$ for all $q \in (q_1, q_2)$.
7. If A is strictly increasing on Q then, $N(A, A(q))$ is Lipschitz in q.
8. $N(A_1, a) = N(A_2, a)$ if $\int_Q \mid A_1(q) - A_2(q) \mid f(q) \cdot dq = 0$.
9. N is bounded for all A
10. Define $A_t(q)$ to be the function $A(q)$ on $[q_{\text{min}}, q_t)$ and a_{max} on $[q_t, q_{\text{max}}]$. $N(A_t, a_{\text{max}})$ is an increasing function of the parameter t.
11. $N(A,a) > 0$.

Say that $N \in \mathcal{N}(i, j - k)$ if N satisfies conditions i and j through to k, e.g. $N \in \mathcal{N}(1, 3 - 5)$ means $N \in \mathcal{N}(1)$, $\mathcal{N}(3)$, $\mathcal{N}(4)$, $\mathcal{N}(5)$.

The intuition behind $\mathcal{N}(1)$ is explained in Fig. 1.

$\mathcal{N}(2)$ states that small differences in perceived qualities should lead to small differences in fitness.

$\mathcal{N}(3)$ comes from the assumption that individuals of higher quality are strictly preferred to individuals of lower quality. This guarantees that PNEs to the models are separable.

The intuition behind $\mathcal{N}(4)$ and $\mathcal{N}(5)$ is explained in Fig. 2.

$\mathcal{N}(6)$ represents the situation in which the population signalling strategy, as long as it is separating, does not affect the population structure or the receiver strategy. This is not to say that a particular receiver strategy is assumed—receiver strategies can still be free to evolve under this condition. All this condition states is that the optimal receiver strategy is decoupled/independent from the male strategy. An example of such a situation is given in section 5.2. This condition is relaxed in section 2.3 and thereafter.

$\mathcal{N}(7)$ is of technical importance only. Without this assumption, unique solutions to various differential equations that appear throughout the paper cannot be guaranteed. Uniqueness is required because the differential equations are used to define functionals.

$\mathcal{N}(8)$ represents the intuition that the receiver strategy should be unaffected by differences in the signalling population that have zero probability of being observed.

$\mathcal{N}(9)$ is the assumption that there is an upper bound on possible fitness gains that may be obtained by signalling.

$\mathcal{N}(10)$ is used in models of bounded signalling. If $N \in \mathcal{N}(10)$ it satisfies the intuition that the higher the expected quality of individuals signalling at the highest possible level, the higher their expected payoff.

$\mathcal{N}(11)$ is a necessary assumption in multiplicative models to avoid Desperado effects (Grafen 1987; see also section 5.3). From a mathematical perspective it allows a logarithmic transformation to draw a correspondence between multiplicative and additive models.

These conditions are satisfied by the following 'pool-comparison' or best-of-n strategy for female choice which has been assumed in various theoretical treatments of sexual selection (e.g. O'Donald 1980; Janetos 1980; Seger 1985; Real 1990):

> Females randomly sample n males, from a pool of males which is truly random in composition with respect to the total population. Females choose to mate with the male who is advertising at the highest level, and if more than one male advertises at the highest level observed, the female chooses randomly from those males advertising at the highest level. The advertising level of males in the population is assumed not to affect the distribution of male qualities.

This strategy gives a mathematical formulation equivalent to an n-player Opponent Independent Cost Game (OICG) (Parker 1979). N under these conditions is given by:

$$N_n(A,a) = \sum_{i=1}^{n} \frac{(n-1)!}{(i)!(n-i)!} \left(\int_{\{q;A(q)<a\}} f(q) \cdot dq \right)^{n-i} \left(\int_{\{q;A(q)=a\}} f(q) \cdot dq \right)^{i-1}$$

If A is strictly increasing, this reduces to $F^{n-1}(A^{-1}(a))$. Note that the integrals are defined when A is a PNE as PNEs are increasing. It is simple to check that $N_n \in \mathcal{N}(1-6,8,9)$, and if $f(q)$ is bounded where it exists, $N_n \in \mathcal{N}(7)$. See chapter 5 for further details.

In general, conditions $\mathcal{N}(1-5,7-10)$ will be satisfied by models where there is no error in perception or realization of signals and receiver behaviour involves sampling a population and then selecting the individual that advertises at one extreme (i.e. highest or lowest level of advertisement observed), or in models, such as the OICG in which, although there are no receivers, the payoff structure is as if there were receivers behaving in this way. Grafen's (1990a) model of female choice also satisfies conditions $\mathcal{N}(2-5,7-11)$.

One difficulty that is often encountered with signalling models is that there is often no single obvious solution to the problem of the interpretation of signals that are not normally seen in the population. Grafen's solution to the problem was 'local flat extrapolation' The solution chosen here is $\mathcal{N}(1)$. To anticipate results proven later, $\mathcal{N}(1)$ was chosen because it makes N compatible with the War of Attrition (Maynard-Smith 1974) and the Opponent Independent Cost Game (Parker 1979). In section 6.2 it is shown how Grafen's (1990a) model is a special case of the multiplicative fitness partition solved in Propositon 2.3, if his condition is replaced by $\mathcal{N}(1)$. Moreover, the result obtained turns out to be the same as that obtained under the assumption of 'local flat extrapolation', except in the case of bounded signals. As indicated in Siller (1997b), Grafen's (1990b) models of handicap signalling can only support separating signalling ESSs due to his assumption that out of equilibrium signals are interpreted by 'local flat extrapolation'. If, instead, it is assumed that out of equilibrium receiver behaviour leads to $N \in \mathcal{N}(1)$ then a signalling ESS exists even when a significant proportion of high quality individuals signal at $a_{\max}$. Different assumptions again, are considered in the model solved in Proposition 2.4.

2.2.4 ESSs are Strictly Increasing in Quality

Lemma 2.3 *Assume the conditions of Lemma 2.1 and that $N \in \mathcal{N}(4)$ then if A is a PNE to the game defined by equation (2.1) it is strictly increasing.*

Note that it is implicit in the condition $N \in \mathcal{N}(4)$, that $f(q) \neq 0$ almost everywhere in Q.

Proof: From Lemma 2.1 we know that A is increasing. To see that A must be strictly increasing, suppose that there is an interval $\mathcal{J} \subseteq Q$ on which A is constant, say $A(\mathcal{J}) = \{a'\}$. Let $q' = \sup\{q; q \in \mathcal{J}\}$, then, as $N \in \mathcal{N}(4)$ and by the continuity of C in a, it will pay individuals of qualities $q \in \mathcal{J}$, to signal marginally higher than a', the difference in payoff being at least:

$$V(A,q)\epsilon - (C(A,a'+\delta,q) - C(A,a',q))$$

where $\delta > 0$ is suitably small. □

A corollary of this proof is that not all signalling strategies have PBRs. To see this, consider a signalling strategy that is qualitatively similar to the one illustrated in Fig.2, i.e. a strategy which is increasing with a single flat between q_1 and q_2. Assume that $N(A,a)$ is differentiable in a for all $a \in (a_{\min}, a') \cup$

$(a', a_{\max})$. Further assume that, for some $q \in [q_1, q_2]$, $C_2(A,a,q)/V(A,q) < N_2(A,a)$ for all $a \in (a_{\min}, a')$, and that $C_2(A,a,q)/V(A,q) > N_2(A,a)$ for all $a \in (a', a_{\max})$. Under these assumptions, for all $\delta > 0$:

$$\begin{aligned} P(A, a'+\delta, q) &< P(A, a'+\delta/2, q) \\ P(A, a'-\delta, q) &< P(A, a'-\delta/2, q) \end{aligned}$$

Thus, the only possible PBR to A for an individual of quality q is a'. However, following reasoning similar to the proof of Lemma 2.3, if $N \in \mathcal{N}(4)$ then we know that there exists a $\delta' > 0$ so that for all $0 < \delta < \delta'$, $P(A, a'+\delta, q) > P(A, a', q)$, which negates the possibility of a' being a PBR to A for individuals of quality q.

2.2.5 ESSs are Absolutely Continuous

Lemma 2.4 *Assume the conditions of Lemma 2.1, that* $N \in \mathcal{N}(2,4)$ *and:*

$$C_2(A,a,q) > 0 \quad a.e. \tag{2.5}$$

If A *is a PNE to the game defined by equation (2.1) it is continuous.*

Proof: From the previous lemma, A may be assumed to be strictly increasing. Suppose there exists $q' \in Q$ at which A is discontinuous, then at least one of the following is the case:

$$\begin{aligned} \lim_{q \uparrow q'} A(q) &= a_\uparrow < A(q') \\ \lim_{q \downarrow q'} A(q) &= a_\downarrow > A(q') \end{aligned} \tag{2.6}$$

which implies that $a_\uparrow < a_\downarrow$. As $N \in \mathcal{N}(2)$, and A is strictly increasing:

$$N(A, a_\uparrow) = N(A, a_\downarrow).$$

Thus, as $N \in \mathcal{N}(2)$ there exists $\delta' > 0$ so that if $0 < \delta < \delta'$:

$$V(A,q'+\delta)(N(A,a_\uparrow)-N(A,A(q'+\delta)))-C(A,a_\uparrow,q'+\delta)+C(A,A(q'+\delta),q'+\delta) > 0$$

which contradicts the assumption that A is a PNE. □

Lemma 2.5 *Assume the conditions of Lemma 2.1, that* $N \in \mathcal{N}(2,4,7)$, V *is bounded, and that either:*

$$C_2 \geq \kappa > 0 \quad \text{on } [a_{\min}, A(q_{\max})] \times Q$$

or that $C_2 > 0$ *and is continuous on* $[a_{\min}, A(q_{\max})] \times Q$ *(which implies that there exists a* κ *as in the above equation), then if* A *is a PNE it is absolutely continuous.*

Proof: From Lemma 2.3 we may assume that A is strictly increasing. As $N \in \mathcal{N}(7)$ there exists a constant N_L so that:

$$| N(A, A(q_2)) - N(A, A(q_1)) | \leq N_L \mid q_2 - q_1 \mid$$

Suppose that A is not absolutely continuous, then for any λ there exists q_λ and ϵ_λ so that:

$$C(A, A(q_\lambda), q_\lambda) - C(A, A(q_\lambda - \epsilon_\lambda), q_\lambda) > \kappa\lambda\epsilon_\lambda$$

as A cannot be Lipschitz if it is not absolutely continuous. Choose $\lambda > (N_L \sup_Q\{V(q)\})/\kappa$, then we have:

$$\begin{aligned} P(A, A(q_\lambda), q_\lambda) - P(A, A(q_\lambda - \epsilon_\lambda), q_\lambda) &\leq N_L \sup_Q\{V(A,q)\}\epsilon_\lambda \\ &\quad -C(A, A(q_\lambda), q_\lambda) + C(A, A(q_\lambda - \epsilon_\lambda), q_\lambda) \\ &< N_L \sup_Q\{V(A,q)\}\epsilon_\lambda - \kappa\lambda\epsilon_\lambda \\ &< 0 \end{aligned}$$

This contradicts the supposition that A is a PNE. □

2.2.6 Lowest Quality Individuals Signal at Lowest Possible Level

Lemma 2.6 *Assume the conditions of Lemma 2.1, that C satisfies equation (2.5), and that $N \in \mathcal{N}(1,4)$, then if A is a PNE to the game defined by equation (2.1) then $A(q_{\min}) = a_{\min}$.*

Proof: First note that if A is a PNE, A is strictly increasing by Lemma 2.3, as $N \in \mathcal{N}(4)$. Also, if A is a PNE then:

$$V(A, q_{\min})N(A, A(q_{\min})) - C(A, A(q_{\min}), q_{\min}) \geq V(A, q_{\min})N(A, a_{\min}) - C(A, a_{\min}, q_{\min})$$

but as $N \in \mathcal{N}(1)$, $N(A, A(q_{\min})) = N(A, a_{\min})$, and thus:

$$C(A, A(q_{\min}), q_{\min}) \leq C(A, a_{\min}, q_{\min})$$

which, by equation (2.5), implies that $A(q_{\min}) = a_{\min}$. □

2.2.7 PNEs and SNEs are Equivalent

Lemma 2.7 *Assume the conditions of Lemma 2.1. If $V(A,q)$ is measurable in q for every PNE, then every PNE is an SNE. If F is strictly increasing and absolutely continuous, and $N \in \mathcal{N}(1,2,8)$, then every strictly increasing bounded SNE contains a PNE.*

•

Proof: The first claim is obvious. It should be noted that every PNE is comparable to all piecewise monotonic functions.

Assume that $N \in \mathcal{N}(8)$ and suppose A is an SNE and differs from a strictly increasing function on a set of measure zero. Every member of A is a PNE almost everywhere. (Note that A is a set of functions that differ on at most a set of measure zero.) To see this, first note that $P(A, a, q)/V(A, q)$ is continuous in a. Further, as $N \in \mathcal{N}(1,2)$ and each member of A differs from a bounded increasing function on at most a set of measure zero, there exists a PBR of A. Denote this PBR by A^* We have that:

$$\int_Q (P(A, A^*(q), q) - P(A, A_0(q), q))f(q) \cdot dq \geq 0$$

where $A_0 \in \mathcal{A}$. The inequality is strict if and only if:

$$P(A, A^*(q), q) > P(A, A_0(q), q)$$

for a subset of Q that has measure greater than zero (Goffman 1953, p213). This is impossible as A is a SNE. Thus, A_0 is a PNE except possibly on a set of measure zero. The function defined to be $A_0(q)$ wherever A_0 is its own pointwise best response and $A^*(q)$ elsewhere therefore differs from A_0 on a set of measure zero and is thus an element of $\mathcal{A}$. □

2.2.8 Solution to Additive Model

Proposition 2.1 *Let $q_{\max} - q_{\min} < \infty$, $a_{\max} = \infty$, and F be a strictly increasing absolutely continuous function of q (continuity implies that f has no atoms). Suppose that $N \in \mathcal{N}(1-4, 6-9)$ and that V and C are independent of A, satisfy equation (2.2), C is absolutely continuous in a, $C_1(a,q)/V(q)$ is absolutely continuous in q, and that:*

$$C_1(a,q) \geq \kappa > 0, \quad \text{for a.a. } (a,q) \in \mathcal{A} \times Q \tag{2.7}$$

then there exists a unique signalling ESS, $A^*(q)$. Furthermore, A^* is absolutely continuous, strictly increasing and $A^*(q_{\min}) = a_{\min}$.

It should be noted that in this proposition, it has beeen assumed that C is independent of A, and consequently, the variable A has been dropped from C in the statement of the proposition. Thus, $C_1(a,q)$ in the above proposition should be identified with $C_2(A, a, q)$ in the previous lemmas, including Lemma 2.1, which is referred to in the statement of the above proposition.

Proof: The proof is in six parts, labelled for future reference.

[1] Lemmas 2.1 and 2.3-2.5 show that any PNE to the game in question, must be absolutely continuous and strictly increasing. Lemma 2.6 implies that any PNE must satisfy $A(q) = a_{\min}$. Lemma 2.7 shows that every SNE and hence every ESS contains a PNE.

[2] Suppose that A° is a PNE. The dependence of N on A° may be omitted as $N \in \mathcal{N}(6)$ and any PNE is strictly increasing.

[3] Similarly, N may be considered to be a function of q as A^{-1} exists for all strictly increasing A and A° must be strictly increasing as $N \in \mathcal{N}(9)$. (If N was not bounded in a then it would be possible for a PNE, A° to satisfy $\lim_{a\to\infty}(A^\circ)^{-1}(a) < q_{\max}$.) Moreover, the derivative of N with respect to q exists almost everywhere as A° is absolutely continuous by previous arguments and N is absolutely continuous as $N \in \mathcal{N}(7)$.

[4] It is next shown that A° must satisfy:

$$\frac{dA^\circ(q)}{dq} = \frac{V(q)N'(q)}{C_1(A^\circ(q), q)} \quad \text{a.e.} \tag{2.8}$$

To see this, suppose that A is absolutely continuous and does not satisfy equation (2.8), i.e. there exists a set of non-zero measure for which:

$$\frac{dA}{dq} - \frac{V(q)N'(q)}{C_1(A(q), q)} = g(q) \neq 0$$

Clearly, $g(q)$ is integrable, and its integral shall be denoted by $G(q)$. The derivative of $G(q)$ exists almost everywhere and is $G'(q) = g(q)$ almost everywhere. This implies that there exists an interval, $[q_1, q_2]$, for which:

$$\int_{q_1}^{q_2} (V(q)N'(q) - C_1(A(q), q)A'(q)) \cdot dq \neq 0$$

(as the derivative of the integral equals the original function almost everywhere). Assume first that the integral is negative. This implies that there exists an interval of qualities $(q_3, q_2]$ of non-zero measure for which $N'(q)$ exists and is positive, and:

$$\int_{q_1}^{q_+} (V(q)N'(q) - C_1(A(q), q)(A)'(q)) \cdot dq < 0$$

for all $q_+ \in (q_3, q_2]$ and equals zero for $q_+ = q_3$. It follows that $A(q_3)$ is a better strategy than $A(q_+)$ for all $q_+ \in (q_3, q_2]$, because the payoff must be increasing in quality, otherwise an individual could do better by signalling at a level lower than his or her true level (note Lemma 2.2). Thus, as $(q_3, q_2]$ is of non-zero measure, we have shown that A cannot be a PNE.

If the integral is positive a similar argument shows that there exists (q_3, q_2) so that individuals of quality $q_+ \in (q_3, q_2)$ do better by signalling at $A(q_2)$ than at $A(q_+)$.

[5] As $C_1 > \kappa$ the conditions for the global existence and 'uniqueness' theorem (Proposition A.3) are satisfied by equation (2.8) (making arbitrary choices for N' where it is not defined by N) and thus there exists a unique absolutely continuous solution to equation (2.8) with initial condition $A^\circ(q_{\min}) = a_{\min}$, and therefore at most one PNE (up to a set of measure 0) can exist, and hence at most one SNE.

[6] Finally, I show that A° is an ESS. Suppose that A° is not an ESS, then there exists $p, q \in Q$, $A^\circ(p) \neq A^\circ(q)$, so that:

$$V(q)N(p) - C(A^\circ(p), q) \geq V(q)N(q) - C(A^\circ(q), q) \tag{2.9}$$

Suppose that the above inequality is strict for some $p < q$, then, as the derivative exists almost everywhere, it may be assumed that $(A^\circ)'(p)$ and $N'(p)$ exist and:

$$V(q)N'(p) - C_1(A^\circ(p), q)(A^\circ)'(p) < 0$$

Applying the inequality (2.2) gives:

$$V(p)N'(p) - C_1(A^\circ(p), p)(A^\circ)'(p) < 0$$

Moreover, this argument applies to a set of non-zero measure of p by continuity, and this contradicts the definition of A°. A similar contradiction may be obtained for $p > q$.

If the inequality in equation (2.9) is never strict, then a more subtle argument is required. Suppose that equality holds in equation (2.9) for $p < q$ such that $A^\circ(p) < A^\circ(q)$, then for all $\epsilon > 0$, there exists a $0 < \delta < \gamma$ where $A^\circ(p + \gamma) < A^\circ(q)$ so that:

$$\mid p - \rho \mid < \delta \Longrightarrow \frac{1}{V(q)} \int_{\rho}^{q} V(q)N'(r) - C_1(A^\circ(r), q)(A^\circ)'(r) \cdot dr < \epsilon$$

Now:

$$\begin{aligned}
&\int_p^q N'(r) - \frac{C_1(A^\circ(r),r)}{V(r)}(A^\circ)'(r)\cdot dr \\
&= \int_p^q N'(r) - \frac{C_1(A^\circ(r),q)}{V(q)}(A^\circ)'(r)\cdot dr \\
&\quad - \int_p^q \left(\frac{C_1(A^\circ(r),r)}{V(r)} - \frac{C_1(A^\circ(r),q)}{V(q)}\right)(A^\circ)'(r)\cdot dr \\
&< \epsilon - \int_{p+\gamma}^q \left(\frac{C_1(A^\circ(r),r)}{V(r)} - \frac{C_1(A^\circ(r),q)}{V(q)}\right)(A^\circ)'(r)\cdot dr
\end{aligned}$$

Clearly, as ϵ is arbitrarily small and the second term of the last equation is fixed and positive by equation (2.2) we have that:

$$\int_p^q N'(r) - \frac{C_1(A^\circ(r),r)}{V(r)}(A^\circ)'(r)\cdot dr < 0$$

for some $p < q$, which implies that:

$$V(r)N'(r) - C_1(A^\circ(r),r)(A^\circ)'(r) < 0$$

for a set of positive measure, which contradicts the definition of A°. This proves that $A^* = A^\circ$ is an ESS, and that it is unique. □

2.2.9 Weakening the Conditions of Proposition 2.1

1. Equation (2.7) is only a sufficient condition for the existence of an ESS, not a necessary one. The existence of a strictly increasing function, B, that satisfies:

   $$\frac{dB(q)}{dq} > \frac{V(q)N'(q)}{C_1(B(q),q)} \quad \text{a.e.}$$

   is also a sufficient condition, as is the existence of a function $A(q)$ such that:

   $$V(q)(N(q_{\max}) - N(q_{\min})) - C(A(q),q) < 0.$$

   The existence of such an $A(q)$ may be interpreted as signalling having the potential to be more costly than the value of the resources under contest. Grafen (1990b), in his ESS model of the handicap principle, failed to require such conditions; this leads to some interesting results that are considered in sections 4.2 and 6.2

2. The results of the additive model are unaffected by adding a function of q to P. In more generality, the game is qualitatively affected only by transformations that change the values of a which maximize P for a given A and q (assuming that the conditions on C etc. are suitably altered). Thus, monotonic transformations of P, a, and q do not affect the essence of the game, and in particular, exponentiation of P turns the game into a multiplicative model.

3. The uniqueness part of the above result requires an extra condition to be satisfied by N than the existence part of the result. If it is not assumed that $N \in \mathcal{N}(7)$, but only that $N(A,a)$ is absolutely continuous in a, then it is possible that there exists multiple absolutely continuous ESSs

as the conditions of Proposition A.1 are not satisfied. The relaxing of this condition also opens up the possibility that continuous functions other than absolutely continuous ones could be ESSs.

4. Arguments adduced in the proof of Proposition 2.3 show that the above Proposition 2.1 still holds, sans uniqueness, with $N \in \mathcal{N}(6)$ replaced by the condition that $N(A,q) \stackrel{\text{def}}{=} N(A,A(q))$ is uniformly continuous in A under the integral norm, with respect to the set of all strictly increasing A, and C and V being constant with respect to A being replaced by C and V being continuous under the integral norm for all increasing A (i.e. the relevant open sets are the intersection of the usual balls under the integral norm with the set of strictly increasing functions and the set of increasing functions respectively).
5. The situation where quality is normally distributed may be modelled by considering the two point completion of the real line and then taking a homeomorphism to a closed interval of finite length:

$$q \mapsto \begin{cases} 0 & \text{if } q = -\infty \\ \frac{1}{\sqrt{2\pi}\sigma} \int_{-\infty}^{q} \exp\left(\frac{-(x-\mu)^2}{2\sigma^2}\right) \cdot dx & \text{otherwise} \end{cases}$$

being the obvious choice, where μ is the population mean quality and σ the population standard deviation in quality. In fact, the above transformation will work for any distribution on $(-\infty, \infty)$.
6. It is also possible to obtain the above results with cumulative population distributions, F, that are increasing, as opposed to strictly increasing. The only difference would be that the result would then be that A^* is strictly increasing in F as opposed to q. These cases have not been considered because the description of results requires some circumlocution.
7. Equation (2.2) is not the 'natural' condition for Lemma 2.1. The 'natural' condition is:

$$\sum_{i=1}^{2}\sum_{j=1}^{2}(-1)^{i+j}\frac{C(a_i,q_j)}{V(q_j)} < 0 \quad \text{whenever } q_1 < q_2 \text{ and } a_1 < a_2. \qquad (2.10)$$

Similarly, the 'natural' condition for C in Lemma 2.3 is that C is strictly increasing in a. These conditions are equivalent to equations (2.2) and (2.5) if C is absolutely continuous in a and $C_2(A,a,q)/V(q)$ is absolutely continuous in q. All the results still hold under the natural conditions, except absolute continuity and uniqueness, provided that C is absolutely continuous in a. The 'unnatural' conditions have been assumed partially because they are more compact and intuitive, and partially because they are necessary for more advanced results.

2.2.10 Pseudo-Convergence Stability of A^*

As noted in section 1.3.3, the ESS condition is not sufficient to guarantee that, when a population is fixed on a strategy close to the ESS, selection should favour a mutation in the direction of the ESS and disfavour a mutation away from the ESS. That is, the ESS condition is not enough to guarantee that an ESS is an evolutionary attractor.

Eshel & Motro (1981) have suggested calling an ESS strategy a continuously stable strategy (CSS), if it has a second property called m-stability (Taylor 1989) or convergence stability (Christiansen 1991). Convergence stability guarantees that an ESS is an evolutionary attractor.

Here, I do not attempt to show that A^* of Proposition 2.1 is a CSS, but that there exist evolutionary trajectories along which A^* is an attractor.

Without loss of generality, we may assume that $N_2(A, A(q))$ is constant (note that $N \in \mathcal{N}(6)$), as if this is not the case all we need do is apply a suitable monotonic transformation to $\mathcal{Q}$. Further assume that $C_1(A^*(q), q)/V(q)$ is constant (if it is not a suitable monotonic tranformation of $\mathcal{A}$ will make it so).

Next, suppose that $A^\circ(q)$ is given implicitly by:

$$\frac{dA^\circ}{dq} = \rho(q)\frac{V(q)N_2(A^*, A^*(q))}{C_1(A^*(q), q)}$$

with the initial condition $A^\circ(q_{\min}) = a_{\min}$, where $\rho(q) < 1$ for all q and is integrable (so that the solution to the differential equation exists and is unique). Clearly $A^\circ(q) < A^*(q)$ for all $q > q_{\min}$.

Consider a population fixed on $A^\circ(q)$, and then consider the fitness of a parameterized set of strategies $A^\epsilon(q)$ defined by.

$$A^\epsilon(q) = \begin{cases} A^\circ(q + \epsilon g(q)) & \text{for } q + \epsilon g(q) \leq q_{\max} \\ A^\circ(q_{\max}) & \text{for } q + \epsilon g(q) > q_{\max} \end{cases}$$

where $g(q)$ is an arbitrary non-negative function of q which is positive on a set of measure greater than zero, and ϵ is a free small parameter. It is assumed that for the range of ϵ under consideration $q + \epsilon g(q)$ is strictly increasing in q. Clearly $A^\epsilon(q) = A^\circ(q)$ when $\epsilon = 0$.

The expected fitness of a rare mutant playing $A^\epsilon(q)$ in a population playing $A^\circ(q)$ is then:

$$\begin{aligned} P(A^\circ, A^\epsilon) &= \int_{q+\epsilon g(q) \leq q_{\max}} [V(q)N(A^\circ, A^\circ(q + \epsilon g(q))) - C(A^\circ(q + \epsilon g(q)), q)]f(q) \cdot dq \\ &\quad + \int_{q+\epsilon g(q) > q_{\max}} [V(q)N(A^\circ, A^\circ(q_{\max})) - C(A^\circ(q_{\max}), q)]f(q) \cdot dq \end{aligned}$$

Treating ϵ as a free parameter and differentiating with respect to it:

$$\left.\frac{\partial P(A^\circ, A^\epsilon)}{\partial \epsilon}\right|_{\epsilon=0} = \int_{\mathcal{Q}} [V(q)N_2(A^\circ, A^\circ(q)) - C_1(A^\circ(q), q)(A^\circ)']g(q)f(q) \cdot dq$$

The integral in the above equation is positive. To see this, note that:

$$\begin{aligned} 0 &= N_2(A^*, A^*(q)) - \frac{C_1(A^*(q), q)}{V(q)}(A^*)'(q) \\ &> N_2(A^\circ, A^\circ(q)) - \frac{C_1(A^*(q), q)}{V(q)}\rho(q)(A^*)'(q) \\ &= N_2(A^\circ, A^\circ(q)) - \frac{C_1(A^*(q), q)}{V(q)}(A^\circ)'(q) \\ &\geq N_2(A^\circ, A^\circ(q)) - \frac{C_1(A^\circ(q), q)}{V(q)}(A^\circ)'(q) \end{aligned}$$

The first line of the above equation holds by Proposition 2.1. The second line is obvious by the definition of ρ. The third line follows from the definition of $(A^{\circ})'(q)$. The final line follows from equation (2.2) and the fact that there exists a $q' \leq q$ for which:

$$\frac{C_1(A^{\circ}(q), q')}{V(q')} = \frac{C_1(A^{*}(q'), q')}{V(q')}$$

Therefore $P(A^{\circ}, A^{\epsilon})$ increasing in ϵ in some neighbourhood of $\epsilon = 0$. That is, on this neighbourhood if $\epsilon > 0$ then A^{ϵ} can invade whilst, if $\epsilon < 0$, A^{ϵ} is disfavoured by selection. As $g(q)$ was assumed to be an arbitrary (almost) non-negative function, the set of functions that can and cannot invade A° is considerable. This is congruous with the notion of convergence stability

By similar arguments it is possible to show an equivalent result for a set of functions which are strictly greater than $A^{*}(q)$, that is functions defined in an analogous way to A° except $\rho(q) > 1$ for all q. It should be noted that it is always possible to construct a pair of strategies A_p, A_m, such that:

$$\| A_p - A^{*} \| > \| A_m - A^{*} \|$$

(where $\| \ \|$ represents the integral norm used implicitly above) but for which A_m cannot invade a population playing A_p. Thus a naïve definition of convergence stability is not appropriate for the kind of models outlined in this paper. However, although convergence stability cannot been shown for all functions in some neighbourhood of A^{*}, it is reasonable to consider that A^{*} is convergently stable in at least some sense (cf. 'reachability', section 9.8).

2.2.11 Perceived Quality

The model solved in Proposition 2.1 assumed that the value of the contested resource to the signaller was independent of its perceived quality. For instance, there is some evidence (Burley 1986, 1988; de Lope & Møller 1993) that females may alter their investment in offspring, dependent upon the perceived quality of the male with which they are paired. This situation may be represented by replacing $V(A, q)$ with $V(A, a)$. As with N, there is a potential problem with signals that are not normally seen in the population. A reasonable solution to this problem is to assume that $VN \in \mathcal{N}(1-4, 6-9)$. This encompasses a wide variety of specific conditions on V For example, if $N \in \mathcal{N}(1-4, 6-9)$, $V(A, a) \in \mathcal{N}(6-9)$ absolutely continuous and increasing in a, implies that $VN \in \mathcal{N}(1-4, 6-9)$.

In models with error in perception and/or signalling (sections 4.1 and 5.4), the problem of interpreting unusual signals does not arise (see also Johnstone & Grafen 1993). Situations between the two extremes (actual-quality-dependent payoff, and perceived-quality-dependent payoff) can also be represented; an example of this is given in section 2.3 (see also comment 5 after the proof of Proposition 2.4).

Proposition 2.2 (Perceived Quality Payoffs) *Let* $q_{\max} - q_{\min} < \infty$ *and* F *be a strictly increasing absolutely continuous function of* q. *Suppose that* $VN \in \mathcal{N}(1-4, 6-9)$, *that* C *satisfies:*

$$\begin{aligned} C_1(a, q) \geq \kappa &> 0 \\ C_{12}(a, q) &< 0, \quad \textit{for a.a. } (a, q) \in \mathcal{A} \times \mathcal{Q} \end{aligned}$$

then there exists a unique signalling ESS, $A^*(q)$. Furthermore, A^* is absolutely continuous, strictly increasing and $A^*(q_{\min}) = a_{\min}$.

2.3 D.E. Approach: Multiplicative Models

A general multiplicative models of signalling is outlined in this section. The model of Grafen (1990a) falls squarely into this category (see section 6.2). The framework developed in this paper makes it apparent that the differences between multiplicative models and general additive models are only cosmetic.

It is assumed that the payoff to an individual of quality q, signalling at a level a in a population playing A is given by:

$$P(A, a, q) = V(A, a, q)N(A, a)S(A, a, q)$$

where V and N are as defined in section 2.3.3.

2.3.1 Interpretation of S

S is a general measure of survival. Depending on the precise interpretation of N, it could represent the expected number of contests that an individual could expect to survive to compete in; the chance that an individual survives until the breeding season; the amount of time the individual can expend on advertising for mates at intensity a; or the amount of time spent on a lek in one season; or a combination of all the above. It could even represent the amount of time that an individual expends on searching for mates at an intensity a; thus, this model could be interpreted as a model of search behaviour, about which more will be said later.

2.3.2 Correspondence of Additive and Multiplicative Models

If $N > 0$ for the individuals perceived as signalling at the lowest level, then there is no difference between the additive and multiplicative models. It will be shown that one can change a multiplicative model into an additive model by taking logarithms, and the reverse tranformation can be made via exponentiation. There are reasons for considering multiplicative models separately from additive models: for instance, they provide a more intuitive framework for models of any situation in which the cost is best interpreted in terms of 'survival' Because of this, they also provide a natural setting for the introduction of the effects of costly signalling on the population structure of males (see section 5.3), though the effects on population structure can be included in additive models (see comment 4 of section 2.2.9).

2.3.3 Differences in Assumptions

Before stating the proposition, some new notation needs to be defined and differences between the assumptions about the functions in the multiplicative model and those in the additive models solved so far need to be outlined. It should be noted that these differences are not due to the multiplicative partitioning *per se*, but because the assumption that $N \in \mathcal{N}(6)$ has been discarded to allow for the population signalling strategy to affect costs, value of the resource etc. If $N \in \mathcal{N}(1-9,11)$ and S and V are independent of A, then the multiplicative model is simply solved by applying a logarithmic transformation and then appealing to Proposition 2.1.

It is assumed that V is a multiplicative combination of both actual- and perceived-quality. That is, $V(A,a,q) = V^q(A,q)V^p(A,a)$. It is not assumed that N is fixed for strictly increasing A, which takes account of the possibility, mentioned above, that the population signalling strategy may affect the population structure and the receiver strategy. This results in the need to employ a more technical method of proof than that encountered in previous propositions. Another advantage of this method of proof is that it allows V^q and S (C in additive models) to depend continuously upon A. This allows the representation of the effects of population structure on the value of resources (e.g. fewer competitors might mean that the value of a particular resource is reduced) or changes in likelihood of being preyed upon depending upon the signalling strategies of other individuals in the population (e.g. if predators moved up sound gradients the chance of being preyed upon would be dependent upon the population signalling strategy, not absolute in terms of the level of signal produced).

For the method of proof employed it turns out that V^pN must be continuous in A. This is not possible for $V^pN \in \mathcal{N}(1-4,7-9,11)$ (which is assumed in the proposition). However, as $V^pN \in \mathcal{N}(2,4,11)$ and therefore any ESS is strictly increasing, at equilibrium receivers can infer a signaller's actual quality. In game theoretic terms, the ESS is said to be separating. With this knowledge it becomes possible to alter the form of V^pN for non-separating signaller strategies without affecting the results. In the proposition below $V^p(A,a)N(A,a)$ is sometimes replaced by the composite $V^pN^s(A,q)$. This may be interpreted as the V^pN that would result if receivers could separate signaller qualities when more than one quality of signaller advertised at a given level. Of course, if receivers could actually do this there would be no point in signalling; it is just an assumption that allows a response to be defined for certain strategies that cannot be ESSs. As ESSs are strictly increasing the assumption does not affect them. For strictly increasing A, $V^pN^s(A,q) = V^p(A,A(q))N(A,A(q))$.

V^pN^s can be defined more rigorously. The set of strictly increasing functions on Q is dense in the set of increasing functions on Q. If $V^p(A,q)N(A,q) \overset{\text{def}}{=} V^p(A,A(q))N(A,A(q))$ is uniformly continuous on the set of strictly increasing functions, then we may define $(V^pN^s)(A,q)$ to be the unique continuous extension of $V^p(A,q)N(A,q)$ to the set of increasing functions (Munkres 1975, p269; see comment 4 of section 2.2.9).

2.3.4 Solution to Multiplicative Model

Proposition 2.3 (Multiplicative Model) *Let* $q_{\max} - q_{\min} < \infty$, *$F$ a strictly increasing absolutely continuous function on Q and $V^pN \in \mathcal{N}(1-5,7-9,11)$ and V^pN^s is continuous in A. Suppose that $S(A,a,q)$ is continuous in a, continuous in A under the integral norm, and thrice differentiable for all (a,q) for* *which* $S(a,q) > 0$. *Also suppose that for all* A*:*

$$\begin{aligned} S_2(A,a,q) &< 0, & (2.11)\\ \frac{\partial}{\partial q}\left(\frac{S_2(A,a,q)}{S(A,a,q)}\right) &> 0, \textit{for a.a. } (a,q) \textit{ such that } S(A,a,q) > 0 & (2.12) \end{aligned}$$

and that:

$$\frac{\partial V^p N^s(A,q)}{\partial q} > 0 \quad \textit{for all } A \textit{ and all } q \in Q \tag{2.13}$$

Further suppose that either:

Case 1: *Define* $B_{\inf}(A,q) = \inf\{a; S(A,a,q) = 0\}$. *Suppose that* $B_{\inf}$ *exists for all* A *and is increasing in* q, *and that there exists an increasing function* $B(q)$ *so that* $S(A, B(q), q) = 0$ *for all* q *and for all increasing* A *for which* $a_{\min} \leq A(q) \leq B(q)$. *Finally suppose that:*

$$S_2(A,a,q) \leq \epsilon < 0 \tag{2.14}$$

Case 2: *Assume that there exists* b *so that* $S(A,b,q) > 0$ *for all* Q *and for which:*

$$\frac{V^p N^s(A, q_{\max}) S(A, b, q_{\max})}{V^p N^s(A, q_{\min}) S(A, a_{\min}, q_{\max})} < 1 \tag{2.15}$$

for all increasing A. *Further assume that for each* A, $S(A,a,q)/S_2(A,a,q)$ *is Lipschitz in* a , *and that there exists an integrable function of* q *which bounds the Lipschitz constants for almost all* q.

Under these conditions, there exists at least one signalling ESS. Furthermore, any ESS must be strictly increasing and continuous.

This result has been proven in a multiplicative framework to make the equivalence between it and Grafen's strategic handicap model clear. The proof is, however, more intuitive in the additive framework. In particular, the two cases in the above statement of the proposition turm out to be special cases of a more general formulation.

Proof: Consider the transformation $P^{add}(A,a,q) \equiv \ln(P(A,a,q))$:

$$P^{add}(A,a,q) = (\ln V^p + \ln N) + \ln V^q + \ln S$$

This is well defined as $V^p N \in \mathcal{N}(1)$. It is easily checked that $\ln S$ satisfies the conditions on C and V^q given in the above proposition, and that if $V^p N \in \mathcal{N}(i)$, $i > 1$ then $(\ln V^p + \ln N) \in \mathcal{N}(i)$.

Lemmas 2.1 and 2.3-2.6 may then be applied to conclude that any ESS, A^*, to the multiplicative model must be absolutely continuous and strictly increasing, and that $A^*(q_{\min}) = a_{\min}$.

As has been outlined above, a problem arises when the population structure is allowed to be dependent upon the population signalling strategy, namely the solution to the first order condition for an ESS changes the first order condition; the ESS cannot be simply constructed as the solution to a differential equation as knowledge of the differential equation requires global knowledge of the ESS. An

ESS will be a signalling function that gives rise to the first order condition that generates it. To find such an signalling function requires the use of a fixed point theorem, in this case the theorem due to Schauder (Deimling 1985 (Theorem 8.8) or Saaty & Bram 1964 (p372)):

> Theorem: Let $\mathcal{X}$ be a real Banach Space, $\mathcal{S} \subset \mathcal{X}$ non-empty, closed, bounded and convex, $M : \mathcal{S} \to \mathcal{S}$ be compact and continuous, then M has a fixed point.

A slightly modified version of this theorem will be used in which the convexity condition is replaced by, $\mathcal{S}$ is homeomorphic to a convex set of $\mathcal{X}$ via a homeomorphism h. This can be seen to be a trivial extension of the theorem as quoted by Deimling (1985), as $h(\mathcal{S})$ and $h \circ M \circ h^{-1}$ satisfy the conditions of Schauder's Theorem. The reason for the convexity condition is that it guarantees that there are no 'holes' in $\mathcal{S}$ for a potential fixed point to 'fall into'; the actual shape of the space is of no real concern.

As any ESS to this type of problem must be an absolutely continuous function, the search for an ESS may be restricted to any Banach space that contains these functions, thus set $\mathcal{X}$ to be the Banach space of Lebesgue integrable functions on $\mathcal{Q}$ (Riesz & Nagy 1955), which shall be denoted $\mathcal{L}_1(\mathcal{Q})$. Note that the underlying linear-space of $\mathcal{L}_1(\mathcal{Q})$ is not the linear space induced on the set of Lebesgue integrable functions, $L_1(\mathcal{Q})$, by pointwise addition, but the factorspace:

$$L_1(\mathcal{Q})/L_1^0(\mathcal{Q})$$

where $L_1^0(\mathcal{Q})$ represents the subspace of functions that differ from 0 only on a set of measure zero.

The two cases in the proposition need slightly different treatment.

Case 1: Set:

$$\mathcal{S} = \{A;\ A \text{ increasing, and } a_{\min} \leq A(q) \leq B(q) \text{ for all } q \in \mathcal{Q}\}$$

Define $M(A)(q)$ to be the unique absolutely continuous solution to the differential equation:

$$\frac{dM(A)}{dq} \overset{\text{def}}{=} -\frac{(V^p N^s)_2(A,q) S(A, M(A)(q), q)}{(V^p N^s)(A,q) S_2(A, M(A)(q), q)} \quad \text{a.e.} \tag{2.16}$$

with the initial condition $M(A)(q_{\min}) = a_{\min}$.

Now:

$$\left| \frac{S(A,a,q)}{S_2(A,a,q)} \right| \leq \left| \frac{S(A,a,q)}{\epsilon} \right|$$

and thus S/S_2 is continuous which implies that equation (2.16) is integrable. All this taken together implies that $M(A)(q) < B_{\inf}(A,q)$ almost everywhere. (A function that does not satisfy this may be shown not to satisfy equation (2.16) via a tedious, but simple argument.) This also implies that $M(A)(q)$ is strictly increasing in q. M is well defined and sends $\mathcal{S}$ into $\mathcal{S}$.

Case 2: Set:

$$\mathcal{S} = \{A;\ A \text{ increasing, and } a_{\min} \leq A(q) \leq b \text{ for all } q \in \mathcal{Q}\}$$

Define $M(A)(q)$ to be the unique absolutely continuous solution to the differential equation:

$$\frac{dM(A)}{dq} \overset{\text{def}}{=} -\frac{(V^pN^s)_2(A,q)S(A,M(A)(q),q)}{(V^pN^s)(A,q)S_2(A,M(A)(q),q)} \quad \text{a.e.} \tag{2.17}$$

with the initial condition $M(A)(q_{\min}) = a_{\min}$.

Suppose that $A \in \mathcal{S}$, then $M(A)(q)$ exists and is unique by Proposition A.3 as long as it lies within $[a_{\min}, b] \times \mathcal{Q}$ (note that the generalized Lipschitz condition of Proposition A.1 is satisfied as S/S_2 is Lipschitz and the function it is multiplied by is integrable).

It is now shown that $M(A)(q)$ cannot equal b. Suppose that $M(A)(q)$ exists for $q \in [q_{\min}, q') \overset{\text{def}}{=} \mathcal{Q}'$; $q' > q_{\min}$ by the local result Proposition A.1. We may define for all $q \in \mathcal{Q}'$ the quasi-payoff function:

$$P_M(A,a,q) = \frac{V^pN^s(A,(M(A))^{-1}(a))S(M(A)((M(A))^{-1}(a)),q)}{S(A,a_{\min},q)}$$

(the inverse exists from an argument similar to Case 1) then:

$$\begin{aligned}\frac{dP_M(A,M(A)(q),q)}{dq} &= \frac{\partial V^pN^s(A,q)}{\partial q}\frac{S(A,M(A)(q),q)}{S(A,a_{\min},q)}\\ &+ \frac{V^pN^s(A,q)S_2(A,M(A)(q),q)}{S(A,a_{\min},q)}\frac{dM(A)}{dq}\\ &+ \frac{V^pN^s(A,q)S_3(A,M(A)(q),q)}{S(A,a_{\min},q)}\end{aligned}$$

The first two rows of the right hand side of this equation sum to zero by the definition of $M(A)(q)$. Thus:

$$\frac{d}{dq}\left(\frac{P_M(A,M(A)(q),q)}{P_M(A,a_{\min},q)}\right) = H(A,q)\left(\frac{S_3(A,M(A)(q),q)}{S(A,M(A)(q),q)} - \frac{S_3(A,a_{\min},q)}{S(A,a_{\min},q)}\right) \tag{2.18}$$

where H is a positive function. Suppose that $M(A)(q_b) = b$, then:

$$\frac{P_M(A,b,q_b)}{P_M(A,a_{\min},q_b)} \le \frac{V^pN^s(A,q_{\max})S(A,b,q_{\max})}{V^pN^s(A,q_{\min})S(A,a_{\min},q_{\max})} < 1$$

which contradicts equation (2.18) which implies that the left hand side of the above equation must be greater than 1, as equation (2.12) implies $S_3(A,a,q)/S(A,a,q)$ is increasing in a. This shows that M maps $\mathcal{S}$ into itself. An argument similar to Case 1 shows that $M(A)$ is strictly increasing.

Case 1 and 2: Clearly, as $M(A)$ is a PBR to A whenever A is strictly increasing, a signalling strategy is a signalling ESS of the model if and only if it is a fixed point of M (see proof of Proposition 2.1 for details).

(Note that the image of M contains strictly increasing functions only. Also note that V^q does not appear in the equation for the ESS. The reason for this is obvious if one considers the logarithmic form of the payoff function.)

M is continuous in A, as V^pN^s and S are continuous in A, and M is a compact mapping on $\mathcal{S}$ as $\mathcal{S}$ is compact as it is homeomorphic to the set of increasing functions from a closed interval to another closed interval, which is compact by Lemma 4 of Grafen (1990a).

It has now been shown that the conditions of Schauder's Fixed Point Theorem are satisfied, and therefore at least one fixed point exists. Any fixed point of M is an ESS. □

2.3.5 Extending the Result

1. In the above proposition it is assumed that the value of the resource is separable, i.e. $V = V^p V^q$. Results similar to Proposition 2.3 still hold if this is not true, however equation (2.12) would need to be altered. Similarly, we could assume that the payoff was not purely multiplicative, e.g. $(N(A,a))^{V^q(A,q)} S(A,a,q)$. The proposition would then hold if equation (2.12) was replaced by:

   $$\frac{\partial}{\partial q}\left(\frac{S_2(A,a,q)}{V^q(A,q)S(A,a,q)}\right) > 0, \text{for almost all } (a,q) \text{ such that } S(A,a,q) > 0$$

   which is the multiplicative equivalent of equation (2.2). (A plausible interpretation of exponentiation would be the situation in which males have a limit to the amount of sperm that they can produce in a season, thus as N increases we would not expect the males resulting reproductive success to increase linearly, but to taper off, which is the effect of setting $V^q(A,q) < 1$.)

2. Note that the result is independent of the payoff function up to multiplication by a positive function of q, which is the multiplicative equivalent of adding an arbitrary function of q in the additive case. The result is also independent up to the addition of a function of q as this too does not change the ordering on a-strategies for each q.

3. The condition that $B_{\inf}(A,q)$ is increasing arises naturally if it is assumed that $S_3 \geq 0$ for all (a,q).

4. Equation 2.12 is not the 'natural' condition for Proposition 2.3 in the same way as equation (2.2) is not the 'natural' condition for Lemma 2.1. The 'natural' condition is:

   $$\frac{S(A,a_2,q_1)}{S(A,a_1,q_1)} < \frac{S(A,a_2,q_2)}{S(A,a_1,q_2)} \quad \text{whenever } q_1 < q_2 \text{ and } a_1 < a_2. \qquad (2.19)$$

   which is the condition used by Grafen (1990a) and Johnstone & Grafen (1992). To see that this condition is basically the same as equation (2.12), one needs apply the logarithmic transform to the multiplicative model, and identify $\ln S$ with $-C$ in the additive model; then note that S_2/S is the derivative of $\ln S$ with respect to a and that the logarithm of equation (2.19) is identical with the 'natural' additive condition equation (2.10).

2.3.6 A Counter Intuitive Example

Consider a non-senescent seasonal breeding species. The chance of surviving between each breeding season is assumed to be a product of two factors

$T(a,q) = \hat{T}(a)\check{T}(q)$, where a represents the effort spent on reproduction during each breeding season. Expected future lifetime reproductive success may then be represented:

$$P(A,a,q) = N(A,a) + \sum_{i=1}^{\infty} N(A,a_i)\delta^i \left(\prod_{j=1}^{i} T(a_i, q) \right)$$

where $\delta < 1$ is a discounting factor on future offspring. As individuals do not senesce, the expected future reproductive success looks the same at any age, and thus we may assume that for an optimal strategy $a_i = a$ for all i. This allows expected future reproductive success to be written:

$$P(A,a,q) = \frac{N(A,a)}{1 - \delta T(a,q)}$$

Setting $S = 1/(1 - \delta T)$ we see that expected future reproductive success is in a form compatible with Proposition 2.3. Naïvely, one might expect that the healthiest individuals, that is the individuals for which $\check{T}(q)$ is the highest, should expend most on reproductive success at equilibrium. However:

$$\begin{aligned} S_1(a,q) &= \frac{\delta \hat{T}'(a)\check{T}(q)}{(1 - \delta T)^2} \\ \frac{\partial}{\partial q}\left(\frac{S_1(a,q)}{S(a,q)}\right) &= \frac{\delta \hat{T}'(a)\check{T}'(q)}{(1 - \delta T)^2} \end{aligned}$$

Thus S_1/S is the reverse of equation (2.12). Proposition 2.3 then gives that individuals which are, *ceteris paribus*, the healthiest, should expend the least on reproductive effort each season; they will have the fewest offspring each season etc.

This raises some interesting possibilities. Geist (1971) found a negative correlation between effort expended during the rut in mountain sheep and their overwinter survival. Similarly, he found a negative correlation between horn size and longevity in males. Were these small long lived males actually the fittest?

If females are passively attracted by male signals, for example they move up sound gradients, or if females choose males by the males possession of resources, such as a high quality territory, then the above analysis shows that this could lead to females in effect prefering to mate with the worst males.

2.4 Fixed Point Theorem Approach •

2.4.1 A Lemma about Best Responses

Lemma 2.8 *Let $\mathcal{U}$ be a topological space, $\mathcal{V}$ a compact topological space, and:*

$$P(\cdot,\cdot) : \mathcal{U} \times \mathcal{V} \to \mathbb{R}$$

a function which is continuous in both its variables. If there exists a function: $M : \mathcal{U} \to \mathcal{V}$ which satisfies for all $A \in \mathcal{U}$:

$$P(A, M(A)) > P(A,B) \quad \textit{for all } B \in \mathcal{V} - M(A)$$

then M is continuous.

If P is interpreted as the payoff in a game, then the above lemma may be interpreted as: if payoffs are continuous in the population (or opposition strategy, i.e. the first variable), and there always exists a unique best response to the population strategy for an individual, then this best response ($M(\cdot)$) is continuous in the population strategy. The following proof relies on nets, a generalization of the notion of a sequence (see Munkres 1975, p188). The term 'net' may be replaced by 'subsequence' throughout the proof provided that $\mathcal{U}$ is first countable (e.g. a metric space).

Proof: All we need show is that for every convergent net $\{A_\alpha\}_{\alpha\in\mathcal{I}} \rightarrow A$ in $\mathcal{U}$, the net $\{M(A_\alpha)\}_{\alpha\in I}$ converges to $M(A)$ (Munkres 1975, p188). This shall be done by contradiction.

Suppose that $\{A_\alpha\}_{\alpha\in I} \rightarrow A$, but that $\{M(A_\alpha)\}_{\alpha\in I}$ does not converge to $M(A)$, then there exists an open neighbourhood, $\mathcal{V}_A$ of $M(A)$ and a subnet of $\{A_\alpha\}_{\alpha\in I}$, say $\{A_\alpha\}_{\alpha\in J}$, for which $M(A_\alpha) \notin \mathcal{V}_A$ for all $\alpha \in J$. To see this, first note that as $\{M(A_\alpha)\}_{\alpha\in I}$ does not converge to $M(A)$ there exists an open neighbourhood $\mathcal{V}_A$ of $M(A)$ for which there does not exist $\beta \in I$ so that $\alpha \succeq \beta \Longrightarrow M(A_\alpha) \in \mathcal{V}_A$. Then note that this implies that $\{M(A_\alpha)\}_{\alpha\in I} \cap (\mathcal{V} - \mathcal{V}_A)$ is cofinal in $\{M(A_\alpha)\}_{\alpha\in I}$, as if it were not cofinal there would exist a β with no successor in $\{M(A_\alpha)\}_{\alpha\in I} \cap (\mathcal{V} - \mathcal{V}_A)$ which implies that all β's successors are in $\mathcal{V}_A$. This contradicts our choice of $\mathcal{V}_A$.

Now $\mathcal{V} - \mathcal{V}_A$ is a closed subspace of $\mathcal{V}$ and, therefore, is also compact (Munkres 1975, p165). By a standard result (Munkres 1975, p175), $P(A, \cdot)$ obtains a maximum on $\mathcal{V} - \mathcal{V}_A$, and by the assumption $P(A, M(A)) > P(A, V)$ for all $V \in \mathcal{V} - \mathcal{V}_A$ we see that this maximum is strictly less than $P(A, M(A))$.

Continuity of P in its first variable and the convergence of $\{A_\alpha\}_{\alpha\in I}$ then implies that there exists a subnet labelled by $K \subseteq J$ and a $\beta \in K$ so that for all $\alpha \in K$ for which $\alpha \succeq \beta$:

$$P(A_\alpha, M(A)) > P(A_\alpha, M(A_\alpha))$$

This contradicts the definition of M

To see this final step in the proof, note that as $\mathcal{V} - \mathcal{V}_A$ is compact $\{M(A_\alpha)\}_{\alpha\in J}$ has a convergent subnet. Assume that K labels this subnet and note that:

1. $\{P(A_\alpha, M(A_\alpha))\}_{\alpha\in K}$ converges in the product topology $\mathcal{U} \times \mathcal{V}$ to $P(A_k, M_k)$ some $(A_k, M_k) \in \mathcal{U} \times (\mathcal{V} - \mathcal{V}_A)$.
2. $\{P(A_\alpha, M(A)\}_{\alpha\in I}$ converges to $P(A, M(A))$. •

Then consider the inverses of a pair of disjoint open balls in $\mathbb{R}$ around $P(A, M(A))$ and $P(A_k, M_k)$. □

There is an intuitive way to visualize why Lemma 2.8 is true. Consider a continuously deformable topography, the vertical height of the landscape representing P, and the two surface dimensions representing the space $\mathcal{V}$. $M(A)$ is the summit of the highest hill on the surface. The particular state of the landscape is parameterized by elements of $\mathcal{U}$. The conditions of Lemma 2.8 say that small changes in the deformation parameter lead to only small deformations (i.e. P is continuous in the first variable) and, moreover, there cannot be two 'highest' hills. $M(A)$ being discontinuous is equivalent to a small deformation leading to the highest point in the landscape 'jumping' from one hill to another. However, in the process of one hill growing past another, at some stage the two hills must be of equal height. That is, there must be two 'highest' hills, which is disallowed by the conditions of the lemma.

2.4.2 Additive Model

Proposition 2.4 *Assume that* $q_{\max} - q_{\min} < \infty$, $a_{\max} - a_{\min} < \infty$, *and that* $F(A,q)$ *is increasing and absolutely continuous. Suppose* $V^p(A,a)N(A,a)$ *is continuous in* A *under the integral norm, differentiable in* a *and:*

$$\frac{\partial V^p(A,a)N(A,a)}{\partial a} > 0 \quad \textit{for all } (A,a) \in \mathcal{I} \times \mathcal{A} \qquad (2.20)$$

and is continuous in both variables, where:

$$\mathcal{I} = \{A(q); A(q) \textit{ non-decreasing, and } A(q) \subseteq \mathcal{A}, \textit{a.e.}\} \subset L^1(\mathcal{Q})$$

$L^1(\mathcal{Q})$ *is the set of Lebesgue integrable functions on* $\mathcal{Q}$. *Further assume that* $V^q(A,q) > 0$ *and continuous in* A *and* q:

$$C_2(A,a,q) > 0 \quad \textit{for all } (A,a,q) \in \mathcal{I} \times \mathcal{A} \times \mathcal{Q} \qquad (2.21)$$

and is continuous in A *and* a, *and that:*

$$\frac{\partial}{\partial q}\left(\frac{C_2(A,a,q)}{V^q(A,q)}\right) < 0 \quad \textit{for all } (A,a,q) \in \mathcal{I} \times \mathcal{A} \times \mathcal{Q} \qquad (2.22)$$

then any population ESS, $A^*(q)$, *to the game defined by the equation:*

$$P(A,a,q) = V^q(A,q)V^p(A,a)N(A,a) - C(A,a,q) \qquad (2.23)$$

is increasing in q, *strictly whenever* $A^*(q) \neq a_{\min}$ *or* $a_{\max}$. *Moreover, at least one such ESS exists.*

This proposition provides a significantly shorter proof of the existence of ESSs to the models in sections 2.2 and 2.3 without providing as accurate qualitative descriptions of these ESSs. In chapter 4 it is shown that Proposition 2.4 is fundamental to the analysis of error-prone signalling.

Proof: The proof of the proposition will proceed as follows: first it is shown that for any $A \in L_1(\mathcal{Q})$ there exists a function A_R, unique up to a set of measure 0, which satisfies:

$$P(A, A_R(q), q) \geq P(A,a,q), \quad \text{for all } a \neq A_R(q) \qquad (2.24)$$

with the inequality strict for almost all q. This function is bounded and will be shown to be increasing, hence it is Lebesgue measurable. After checking a few necessary conditions, an application of Schauder's Fixed Point Theorem will then give the existence of an ESS. The proof is broken into seven parts which are labelled. These labels are used for internal reference and are also used for reference in non-mathematical discussion of the proof.

[1]: Let $A_r : \mathcal{Q} \to \mathcal{A}$ be the the relation which consists of all pairs (a_r, q_r) satisfying the inequality (2.24). As $\mathcal{A}$ is compact and P is continuous there is

at least one a_r for each $q_r \in \mathcal{Q}$. Denote $\{(a', q'); (a', q') \in A_r \text{ and } q' = q\}$, by $A_r(q)$.

[2]: Suppose $q_1 < q_2$ and that $a_1 \neq a_{\min}$ or $a_{\max}$. If $(a_1, q_1) \in A_r$ and $(a_2, q_2) \in A_r$ then $a_2 > a_1$. To see this first note that:

$$P_2(A, a, q) = V^q(A, q)\frac{\partial V^p(A, a)N(A, a)}{\partial a} - C_2(A, a, q) \qquad (2.25)$$

As a_1 is an internal maxima and N_2 is not directly dependent upon q it is not possible for $a_2 = a_1$ because of condition (2.22).

Then noting that Lemma 2.1 then gives that $a_2 \geq a_1$ we see that A_r must be strictly increasing except possibly for an initial interval $[q_{\min}, q_{a_{\min}}]$ and a final interval, $[q_{a_{\max}}, q_{\max}]$, where $A_r(q) = (a_{\min}, q)$ and $(a_{\max}, q)$ respectively.

[3]: Next consider the subset $\mathcal{R}$ of $\mathcal{Q}$ defined by

$$\mathcal{R} \overset{\text{def}}{=} \{q; \text{card}(A_r(q)) > 1\}$$

For each $q \in \mathcal{R}$ choose $a_q^+, a_q^- \in A_r(q)$ so that $a_q^+ > a_q^-$, and let $\mathcal{R}_n = \{q; a_q^+ - a_q^- \geq 1/n\}$. Each $\mathcal{R}_n$ has finite cardinality as the $A_r(q_1) \cap A_r(q_2) \subset \{a_{\min}, a_{\max}\}$ for all $q_1, q_2 \in \mathcal{Q}$, and thus by a standard result (Hungerford 1974, p20):

$$\text{card}(\mathcal{R}) \leq \text{card}\left(\bigcup_{n=1}^{\infty} \mathcal{R}_n\right) \leq \aleph_0$$

Thus A_r is a function except on a countable set.

[4]: Let A_R be some choice function (Munkres 1975), that is a function:

$$A_R : \{\{A_r(q)\}; q \in \mathcal{Q}\} \to \bigcup_q \{A_r(q)\}$$

with $A_R(\{A_r(q)\}) \in \{A_r(q)\}$. Identifying the domain of A_R with $\mathcal{Q}$, [3] shows that any choice function differs on a set of measure 0 at most. The final stages of this proof requires the application of Schauder's fixed point theorem which requires that we work in the Banach space $\mathcal{L}^1(\mathcal{Q})$ which is obtained from $L^1(\mathcal{Q})$ by factoring out the subspace generated by the functions that differ from the function $f(q) = 0$ on a set of measure zero. (The norm being: $\|A\| = \int_{\mathcal{Q}} |A(q)| \cdot dq$.) It should be noted that A_R is increasing by [2], and is thus measurable (e.g. Goffman 1953, p182) and is contained in $L^1(\mathcal{Q})$ as it is bounded. Thus, the restrictions of all possible A_R to $\mathcal{L}^1(\mathcal{Q})$ exist and are identical.

[5]: Recall the statement of Schauder's Fixed Point Theorem in section 2.3.

Let $\mathcal{S}$ be the image of $\mathcal{I}$ in $\mathcal{L}^1(\mathcal{Q})$ after the quotient projection. $\mathcal{S}$ is non-empty, convex and compact (hence closed and bounded) by Lemma 4 of (Grafen 1990a). Identify $M(A)$ with the equivalence class of A_R. This is well defined as the payoff function is continuous in A. M is compact as it maps $\mathcal{S}$ onto $\mathcal{S}$. All that is left to show is the continuity of the functional $M : \mathcal{S} \to \mathcal{S}$ defined by $M(A) = A_R$.

[6] Any function that differs from A_R in $\mathcal{S}$, that is a function that differs from A_R in $\mathcal{I}$ on a set of positive measure, say $A_{R'}$, must have a lower global payoff. To see this, first note that the function $(P(A, A_R(q), q) - P(A, A_{R'}(q), q))/V^q(A, q)$

is measurable as it is the sum of measurable functions. As this function is equal to its modulus and it is positive on a set of positive measure we have that:

$$\int_{q_{\min}}^{q_{\max}} (P(A, A_R(q), q) - P(A, A_{R'}(q), q))f(q) \cdot dq > 0,$$

by (Goffman 1953, p213) and thus the equivalence class of the pointwise best response A_R is also the unique global best response. Uniqueness implies that any fixed point of $M(A)$ is an ESS.

[7] Lemma 2.8 can now be used to show that M is continuous. Identify both $\mathcal{U}$ and $\mathcal{V}$ with $\mathcal{S}$. $\mathcal{S}$ is first countable as it is a metric space. Identify the $P(A, B)$ of Lemma 2.8 with:

$$\int_{q_{\min}}^{q_{\max}} (P(A, B(q), q) + C(A, a_{\min}, q))f(q) \cdot dq$$

Note that P is continuous in both its variables. By [6], M satisfies the uniqueness condition required by Lemma 2.8. Thus, M is continuous.

The conditions of Schauder's Fixed Point Theorem have been satisfied, so it may be concluded that there exists at least one $A^*(q)$ which is a best reply to itself. By [6], A^* is an ESS. □

The philosophy behind the above proof is very simple: every continuous function from a compact space to a linearly ordered space obtains its maximum on that space. Therefore, as long as P is continuous we can then define a 'best response' to a given strategy. That is, no matter what the population signalling strategy is, as long as P is continuous, there will always exist at least one best response. (This does not contradict the discussion given after Lemma 2.3 as P was discontinuous in the example given.) Any strategy that is its own best response is a Nash equilibrium (PNE/SNE) and, as in this case, if it is a unique best response it must be an ESS!

The purpose of all the conditions is to insure that the best responses are of a certain form (basically that they are uniquely defined for each population strategy, that they are increasing, and that the best response is relatively stable with respect to small changes in the population strategy), which prevents cyclic or chaotic series of best responses. The conditions imposed upon the variables and functions in Proposition 2.4 are only sufficient conditions. They were chosen partly so that the relationship between Proposition 2.1 and Proposition 2.4 can be seen, and partly so that the effects of more general assumptions can be highlighted by contraposition. In particular:

1. Equation (2.21) can be replaced by the more general condition:

   $$C(A, a_2, q) - C(A, a_1, q) > 0 \tag{2.26}$$

   for all q, whenever $a_1 < a_2$. Under this assumption, C_2 cannot be guaranteed to exist everywhere. This affects part [2] of the proof; it is no longer possible to guarantee that if $a \neq a_{\min}$ and $a \neq a_{\max}$ then $a \in A_r(q)$ for at most one value of q. This means that, under this assumption, ESSs could have flats for values in the interior of $\mathcal{A}$. This affects the logic behind [3], but this can be repaired by an argument similar to Lemma 2.1 using the assumption contained in equation (2.10) below.

2. Equation (2.22) can be replaced by the more general condition, equation (2.10). As mentioned above, this assumption guarantees that [3] holds.

3. We could allow $Q = [-\infty, \infty]$, the two point completion of the real line. The only effect of this is that the derivative from the right (resp. left) at $q = -\infty$ (resp. $q = \infty$) in equation (2.22) naturally limits to zero at the endpoints. This, however, has no effect on the argument in [2].

4. $a_{\max} = \infty$. It can be seen that the proof is unaffected after applying a homeomorphism sending $[a_{\min}, \infty]$ to $[0, 1]$, as long as it is assumed that signalling at ∞ makes sense. If this does not, then all that is required is that there exists a' for which $\sup_{(A,a)} N(A, a) < \inf_A C(a', q_{\max})/V(q_{\max})$. From a 'biological perspective' at least one of these must hold.

5. The most surprising extension of the above result, however, is that the existence of an increasing ESS requires only that $V^p(A^\circ, A(q))N(A^\circ, A(q))$ is measurable for all $A, A^\circ \in \mathcal{I}$. In particular, an increasing ESS exists even when the conditions on V^pN are relaxed so as to allow $V^p(A, a)N(A, a)$ to be decreasing in a over some or all of $\mathcal{A}$. The proof of this result is basically the same as the proof of Proposition. See Corollary C.3 below.

Corollary 2.5 *Assume the conditions of Proposition 2.4, except equation (2.20) which is relaxed to the condition that* $V^p(A, a)N(A, a)$ *is continuous in* A *and continuous in* a *for all* $A \in \mathcal{I}$, *and* $V^p(A^\circ, A(q))N(A^\circ, A(q))$ *is measurable for all* $A, A^\circ \in \mathcal{I}$. *Under these conditions, there exists at least one increasing ESS to the model defined by equation (C.4).*

Proof: Equation (2.20) and its implications only effect the results of parts [2] and [3] of the proof of Proposition 2.4. The following arguments will use, without redefinition, notation used in the proof of Proposition 2.4.

Equation (2.20) was used in [2] to show that $A_r(q)$ must be strictly increasing in the interior of $\mathcal{A}$, as opposed to just being increasing. Apart from this result *per se*, [2] is only used in part [3], in which it is shown that A_r is a function almost everywhere. This same result can be obtained, if A_r is only increasing (which it must be by Lemma 2.1), by noting that equation (2.22) implies that no $a \in [a_{\min}, \sup A_r(q))$ can be in $A_r(q')$ for all $q' > q$ (where $[a_{\min}, a_{\min})$ is interpreted to mean the empty set). □

The relaxation of the conditions on V^pN means that it can no longer be guaranteed that every ESS is strictly increasing on $(a_{\min}, a_{\max})$. In particular, if $V^p(A, a)N(A, a)$ is decreasing for all $a \in \mathcal{A}$, for all $A \in \mathcal{I}$, then the only ESS is $A^*(q) = a_{\min}$ for all $q \in Q$.

2.4.3 Multiplicative Model

Assume the payoff to an individual of quality q, signalling at a level a in a population playing A is given by:

$$P(A, a, q) = V^q(A, q)V^p(A, a)N(A, a)S(A, a, q)$$

Noting that equation (2.25) and the arguments immediately following are unaffected by the addition of a function independent of a to P, it follows by substituting the logarithmic forms of the relevant functions that Proposition 2.4 provides a proof of the existence of signalling ESSs for multiplicative models provided $V^p(A,a)N(A,a)$ satisfies the conditions imposed on N in the proposition, S satisfies:

$$S_2(A,a,q) < 0 \tag{2.27}$$

$$\frac{\partial}{\partial q}\left(\frac{S_2(A,a,q)}{S(A,a,q)}\right) > 0 \tag{2.28}$$

wherever $S(A,a,q) > 0$, and $B_{\inf}(A,q)$ (defined in Case 1 of Proposition 2.4) is increasing. Equation (2.27) is the equivalent of equation (2.21) in the additive model and equation (2.28) is the equivalent of equation (2.22).

2.5 Classes of Equilibria

The assumptions made on N in sections 2.2-2.3 resulted in only one qualitative type of ESS (though see section 4.2 for a second type of ESS). Small changes in these assumptions can lead to many other types of ESS. For any increasing function, a model that satisfies the weakened conditions of Proposition 2.4 may be constructed for which it is an ESS (see below); therefore, as any ESS must be increasing, the set of possible ESSs is identical with the set of increasing functions on $\mathcal{Q}$. All increasing functions may be decomposed into a sum of three functions: an absolutely continuous function, a saltus function, and a continuous function which has a zero derivative almost everywhere (Riesz & Nagy 1955).

The following six examples encompass the basic features of ESSs to the model solved in Proposition 2.4, though any given ESS may have more than one of these features (as long as they are not mutually exclusive), e.g. it is possible for an ESS to have the feature that $A(q_{\min}) > a_{\min}$ (Ex. 3) and an infinite number of discontinuities (Ex. 5). Graphs of the ESSs are in Fig. 3, and the constructions are outlined below.

The method used to construct these examples is the inverse of the problem as stated in the proposition. An advertising function, $A(q)$ is chosen, and it is then shown that a relative cost function, $C(A,a,q)/V^q(A,q)$, can be constructed, that satisfies the conditions stated after Proposition 2.4, for which A is an ESS. After the examples it is shown how Ex 's 1-5 may constructed so that they satisfy the smoother conditions of Proposition 2.4. Ex 6 requires either that C/V^q does not satisfy the smoothness of conditions of Proposition 2.4, or that V^pN does not satisfy equation (2.20).

Ex. 1: Let A be given by:

$$A(q) = \begin{cases} a_{\min} & q \in [q_{\min}, q_c) \\ (q - q_c) + a_c & q \in [q_c, q_{\max}] \end{cases}$$

Let $a_{\max} > q_{\max} - q_c + a_c$; then $N_2(A,a)$ obtains a maximum, $i_{\max}$, and a minimum, $i_{\min}$, on $\mathcal{A} \times \mathcal{Q}$ as it is continuous and $\mathcal{A} \times \mathcal{Q}$ is compact. Moreover, $i_{\min} > 0$ as N_2 is always greater than 0. Assume that $V^q = V^p = 1$. Let $c_q(a)$ be given by:

$$c_q(a) = \begin{cases} \frac{i_{\min}}{q - q_{\min} + 1 + \varepsilon} & a < A(q) \\ \frac{i_{\max}(q_{\max} - q_{\min} + 1 + \varepsilon)}{q - q_{\min} + \varepsilon} & a \geq A(q) \end{cases}$$

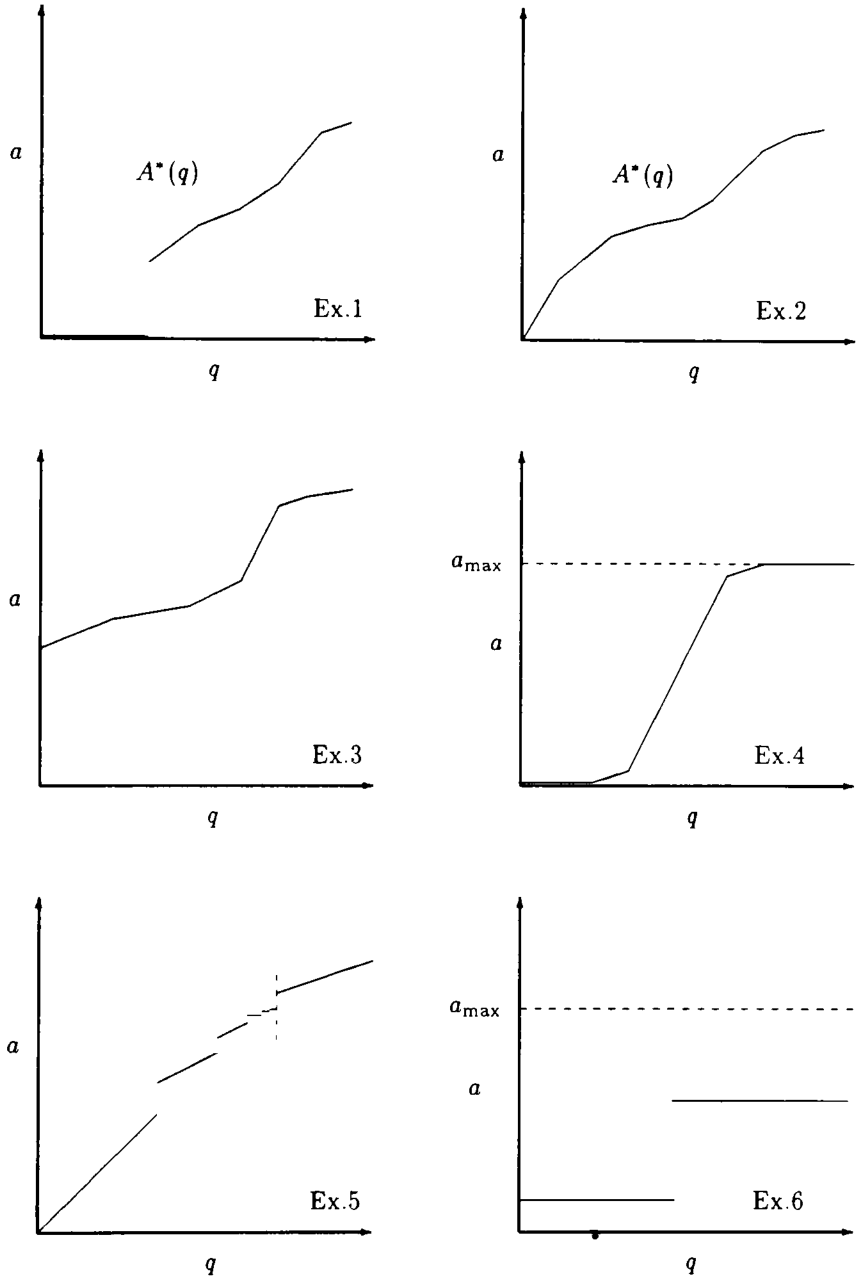

Figure 3: *Examples of the possible forms of ESSs to the game solved in Proposition 2.4. Examples Ex. 1 to Ex. 6 of section 2.5 have ESSs qualitatively similar to the equivalently labelled graphs.*

where ε is a positive constant. Then define:

$$C(A, a, q) = \int_{a_{\min}}^{a} c_q(b) \cdot db,$$

with the condition $C(A, a_{\min}, q) = 0$. Clearly, C satisfies the conditions stated after the proposition as it is of the form $(k_1 a + k_2)/(q + k_3)$, for suitably small balls centred on (a, q), almost everywhere, where k_i are constants dependent upon a and q. Moreover, $P(A, a, q)$ is strictly increasing in a for $a < A(q)$ and strictly decreasing for $a > A(q)$. Thus, $A(q)$ is its own best response. (Note that C has not been defined for arbitrary A. The trivial extension $C(A_i, a, q) = C(A, a, q)$ for all A_i shows that this is unproblematic.)

Ex. 2: This follows by setting $a_c = a_{\min}$ in Ex. 1.

Ex. 3: This follows by setting $q_c = q_{\min}$ in Ex. 1. It should be noted that there is no restriction upon how large a_c may be. Thus, all individuals may advertise at a high level relative to the differences between individuals.

Ex. 4: Let A be given by:

$$A(q) = \begin{cases} a_{\min} & q \in [q_{\min}, q_c) \\ (a_{\max} - a_{\min})\frac{q - q_c}{q_d - q_c} + a_{\min} & q \in [q_c, q_d] \\ a_{\max} & q \in (q_c, q_{\max}] \end{cases}$$

Assume that $V^q = V^p = 1$ and construct $C(A, a, q)$ Ex. 1.

Ex. 5: Let A be given, by the following:

$$A(q) = \begin{cases} (q - q_{\min}) + a_{\min} + k_n(a_c - a_{\min}) & q \in [q_{\min} + k_n q_s, q_{\min} + k_{n+1} q_s) \\ (q - q_c) + a_c & q \in [q_c, q_{\max}] \end{cases}$$

where n ranges over the non-negative integers, $k_n = (2^n - 1)/2^n$, and $q_s = (q_{\max} + q_{\min})/2$ Assume that $V^q = V^p = 1$ and construct $C(A, a, q)$ as in Ex. 1.

Ex. 6: Let A be given by:

$$A(q) = \begin{cases} a_c & q \in [q_{\min}, q_c) \\ a_d & q \in [q_c, q_{\max}] \end{cases}$$

Assume that $V^q = V^p = 1$ and construct $C(A, a, q)$ as in Ex. 1.

It is possible to replace the cost function in Ex.'s 1-5 with a C which satisfies the conditions of Proposition 2.4. A simple method is as follows: First note that any advertising ESS must be strictly increasing when $A(q) \in (a_{\min}, a_{\max})$. If $a' \in (A(q_{\min}), A(q_{\max}))$ and there exists q' so that $a' = A(q')$, set $A_t^{-1}(a') = q'$ Denote $[A(q_{\min}), A(q_{\max})]$ by $\mathcal{A}_A$. If $a' \in \mathcal{A}_A$ but there does not exist a q for which $a' = A(q)$, then, set $A_t^{-1}(a') = \inf\{q; A(q) > a'\}$, and set $C_2(A, a', q') = N_2(A, a')$. This defines a continuous path in $\mathcal{A} \times \mathcal{Q}$, denoted by A_t, from $A(q_{\min})$ to $A(q_{\max})$, which has a uniquely defined inverse from $\mathcal{A}_A \to \mathcal{Q}$. Then set:

$$\frac{C_2(A, a, q)}{V^q(A, q)} = \frac{\partial V^p(A, a) N(A, a)}{\partial a} \left(1 + \left(\frac{A_t^{-1}(a) - q}{q_{\max} - q_{\min} + \epsilon}\right)\right)$$

on $\mathcal{A}_A \times \mathcal{Q}$ where $\epsilon > 0$. For $a > \mathcal{A}_A$ replace $A_t^{-1}(a)$ with $q_{\max}$ and for $a < \mathcal{A}_A$ replace $A_t^{-1}(a)$ with $q_{\min}$. Simple calculation shows that this defines a suitable C/V^q

2.6 Number of Equilibria

A serious failing of Proposition 2.3 is that although it guarantees the existence of at least one ESS, it does not tell us how many ESSs there are, unlike Proposition 2.1 which guarantees that ESSs are unique. Without any further analysis, we cannot be certain that there are not an infinite number of ESSs to the model solved in Proposition 2.3. The following two examples shows that there can exist an arbitrarily large number of ESSs to a game which satisfies the conditions of Propostion 2.3

Example 1: The following example is actually a method for constructing a model whose set of ESSs contains a finite number of given functions, $\{A_1, \ldots, A_n\}$, which satisfies $A_i(q_{\min}) = a_{\min}$ for every i.

First, choose $V^p(A_i, a)N(A, a)$ arbitrarily, and for each A_i set:

$$\frac{C_2(A_i, a, q)}{V^q(A_i, q)} = \frac{\partial V^p(A_i, a)N(A_i, a)}{\partial a}\left(1 + \left(\frac{A_i^{-1}(a) - q}{q_{\max} - q_{\min} + \epsilon}\right)\right)$$

where $\epsilon > 0$. For $a \geq a_{\max}$ replace $A^{-1}(a)$ with $q_{\max}$. Integrating over a with arbitrary initial conditions provides a C/V^q which satisfies the conditions for A_i to be an ESS.

These n functions can be extended to a cost function for the entire set of increasing signalling strategies by setting:

$$C(A, a, q) = \sum_{i=1}^{n}\left(\frac{\prod_{j \neq i} \|A - A_j\|}{\sum_{k=1}^{n} \prod_{j \neq k} \|A - A_j\|}\right) C(A_i, a, q)$$

which is seen to be continuous in A under the integral norm, $\| \quad \|$. If C is independent of A, then a construction similar to the above, only applied to N, shows that there exist a set of N for which there exists multiple equilibria.

Example 2: The following example has an uncountable number of ESSs. Set $a_{\min} = 0$, and assume that the game:

$$P(A, a, q) = V^q(A, q)V^p(A, a)N(A, a) - C(A, a, q)$$

satisfies the condtions of Proposition 2.3. We know that there exists at least one ESS to this game. Choose one ESS, say A^*, set $A_t^*(q) = tA^*(q)$ for all $t \in [\epsilon, \infty)$ and define:

$$\hat{C}(A_t^*, a, q) \stackrel{\text{def}}{=} \frac{1}{t}C(A^*, a, q)$$

and extend this to all the set of all increasing functions from Q to $[0, a_{\max}]$ by setting

$$\hat{C}(A, a, q) \stackrel{\text{def}}{=} \hat{C}(A_t^*, a, q)$$

whenever $\| A_t^* \| = \| A \|$ and by setting:

$$\hat{C}(A, a, q) \stackrel{\text{def}}{=} C(A_\epsilon^*, a, q)$$

whenever $\| A_\epsilon^* \| \geq \| A \|$. Note that this extension is continuous in A as for all norms $\| x - y \| \geq | \| x \| - \| y \| |$. Setting:

$$\begin{aligned} \hat{V}^q(A, q) &\stackrel{\text{def}}{=} V^q(A^*, q) \\ \hat{V}^p(A, a) &\stackrel{\text{def}}{=} V^p(A^*, a) \\ \hat{N}(A, a) &\stackrel{\text{def}}{=} N(A^*, a) \end{aligned}$$

for all A, a, and q, we see that for all $t \in [\epsilon, \infty)$, $A_t^*(q)$ is a fixed point of equation (2.17) for the game defined by:

$$\hat{P}(A, a, q) = \hat{V}^q(A, q)\hat{V}^p(A, a)\hat{N}(A, a) - \hat{C}(A, a, q) \qquad (2.1)$$

Therefore the set of ESSs to the game defined by equation (2.1) contains A_t^* for all $t \in [\epsilon, \infty)$.

3 Receivers, Genetics, Environmental Reaction

3.1 Introduction

In chapter 2 it was assumed that the benefits accrued by signallers were increasing in the level of signal exhibited. This assumption presupposes that receivers should 'reward' higher signals. Previous models of sexual selection show that this may not be the case at equilibrium (e.g. Kirkpatrick 1985).

The costs of receiving the signal, or sampling the signallers, must be repaid by some benefit to the receiver. Therefore, to model a signalling/receiving system faithfully we should consider what is best for receivers as well. Clearly, there is much scope for feedback in such a system. For instance, if a new signalling strategy invades a population then it might affect both the absolute and relative numbers of high and low signallers, e.g. via S in the multiplicative model. This may alter the costs to receivers of sampling the signallers, which in turn may alter their optimal strategy, and so forth.

A change in the population signalling strategy may have other effects. For example, if a predator hunts vocal signallers by travelling up sound gradients, then the probability that a signaller vocalizing at an intensity a is hunted will be affected by the power with which other signallers in the population vocalize. Furthermore, a population of loud vocalizers might be easier to hunt than quiet ones, so a change in the population signalling strategy could affect predator density, which in turn could affect the density of signallers

If quality is at least partially genetically determined, then population signalling and receiving strategies are likely to have effects upon the equilibrium distribution of both signallers' and receivers' distributions of genetic quality, which in turn affect the value of the signalling and receiving strategies. Grafen's (1990a) model of sexual selection supposed that there was variance in male quality, but that the distribution of male quality was independent of the male and female strategies... an assumption unlikely to be true even if the quality was not heritable.

In Propositions 2.3 and 2.4, V, N, and S (or C) were allowed to be continuously dependent upon the population signalling strategy, A. That is, the costs and benefits of signalling were allowed to be relative to the population strategy. This is enough to represent effects which are unilateral or nearly so. However, to provide a completely convincing analysis of the feedback considerations outlined above, it would be better if explicit models of feedback phenomena could be included in the signalling model. The purpose of the following is to indicate how such inclusion can be achieved. Explicit examples applying the methods outlined here are given in chapter 5.

3.2 Receivers and the General Modular Method

In this section a general method of incorporating explicit models of systems that interact with the population of signallers is outlined. However, to facilitate exposition, the method is described with particular reference to the effects of receiver strategies. The description given here is quite abstract. Detailed applications/calculations are given in chapter 5 and section 6.2.

Let D denote a receiver strategy, and $\{D, A\} \in \mathcal{D} \times \mathcal{S}$ represent a receiver/signaller pair of strategies. If it is assumed that no signalling strategy is precluded by a particular receiving strategy and vice versa, then $\{D, A\}$ is an ESS if and only if D is an ESS for receivers in a population in which signallers play A, and A is an ESS for signallers in a population in which receivers play D (recall the discussion of this point in section 1.7).

Clearly, N depends upon the strategy that receivers use and, in many cases, the receiver strategy will depend upon the strategy of the signallers. This implies that the best response of a receiver to a population of signallers is dependent upon the signallers' strategies, and vice versa. Thus, the best response of the receivers to the signallers changes the optimum strategy of the signallers, a situation very similar to that encountered in the multiplicative model of section 2.3. In attempting to solve the mathematics, one is left with a chicken and egg situation: one needs to know the optimal signaller strategy to know the optimal receiver strategy, but one needs to know the optimal receiver strategy to know the optimal signaller strategy.

There is a solution to this problem, and it is basically a trivial extension of the method employed in Propositions 2.3 and 2.4. The idea is to construct a combined space of receiver and signaller strategies, $Z \times \mathcal{Y}$ and then look for fixed points of the map:

$$(M_D \times M_A) \circ \Delta(\{D, A\})$$

where M_D is, usually, the 'best response' of receivers to the signaller and receiver strategies played by the rest of the population, M_A the best response of signallers to the signaller and receiver strategies played by the rest of the population, and Δ the duplication map:

$$\Delta\{D, A\} \rightarrow \{D, A\} \times \{D, A\}$$

In most circumstances one should expect small changes in receiver strategy to shift the optimum signaller strategy by a small amount, and vice versa, which suggests the application of fixed point theorems.

The above can be done implicitly. For example, the analysis in sections 2.3 and 2.4 would be unchanged if, instead of assuming a fixed receiver strategy, it was assumed that the signallers payoff, $P(A, \cdot, \cdot)$, was that which would arise if receivers played the optimal response to a population of signallers playing A. This is the approach that was taken by Grafen (1990a) in his model of the strategic handicap principle.

3.3 Genetics

Grafen's (1990a) strategic handicap model assumed that the quality that was being indicated by the handicap trait was not genetic, and to my knowledge no game theory models of the handicap principle have attempted to deal with heritable quality. This is unfortunate as one of the main kind of benefits that females might obtain by selecting males bearing strategic signals (e.g. handicap traits) is good genes (Williams 1966; Hamilton & Zuk 1982). The reason game theory models have not included the 'genetics of quality' are manifold, but the most pressing of these is the fact that there is feedback between the distribution of quality genotypes and signaller and receiver strategies. In the following it is indicated how the modular approach may be applied to incorporate genetics of quality into strategic signalling models.

First, it will be useful to recall some aspects of the analysis of this paper. First, the models supplied here make little attempt to explain how signalling and receiving arise in a population. Second, although there are no assumptions about the number of loci involved in determining the strategic signal and receiver strategy, each population strategy is assumed to be genetically monomorphic (though there is no reason in principle why the techniques outlined below could not be extended to deal with a constant or periodic supply of additive genetic variance in the signalling and receiving traits). Together, these assumptions allow us to avoid most of the problems of genetic covariances and linkage etc. (see Matessi & Di Pasquale 1996 and chapter 9).

The following are two simple genetics modules, and not all questions raised by them are answered (e.g. in the discrete module, only cursory consideration is made of whether the distribution of quality genes at equilibrium is stable or unstable). More complex/explicit models can be constructed in which these questions can be answered, but this would require a substantial divergence from the main thrust of this paper. The purpose of the modules outlined here is to provide an indication of how the problem of genetics may be approached.

3.3.1 Continuous Distributions of Genotypes

It is standard in quantitative genetic models of sexual selection (Lande 1980, 1981; Kirkpatrick 1985, 1986; Pomiankowski et al. 1991; Iwasa et al. 1991) to assume that there is a continuous distribution of quality genotypes with no atoms of probability and that the additive genetic variance of quality is non-zero; the additive variance that is lost due to differences in fitness is replaced by new mutations. It is also assumed that the relative fitness of quality genotypes does not change too much in any one generation.

It is reasonable to assume that each pair of population receiving/signalling strategies, $\{D, A\} \in \mathcal{D} \times \mathcal{S}$, gives rise to a unique stable equilibrium distribution of genotypes, $g(q) = G(\{D, A\})(q)$ (recall that it is assumed that g has no atoms of probability). This distribution is the balance reached between the loss of additive genetic variance due to selection, and the increase due to mutation.

It is also reasonable to assume that G is continuous in $\{D, A\}$, as a small change in the population's signalling and receiving strategies would seem unlikely to have a large effect on the equilibrium distribution of qualities. Denote by $\mathcal{G}$ the set of equilibrium strategies; $\mathcal{G} = G(\mathcal{D} \times \mathcal{S})$.

Under the assumption that sexes of offspring are assigned randomly, that quality is unaffected by loci on sex chromosomes, and that male and female ploidies are the same, the male and female zygotic quality genotypes are identically distributed. Thus, the state of the population is an element of the space $\mathcal{D} \times \mathcal{S} \times \mathcal{G}$. Non-random assignment of sex, different ploidies of sexes, and quality being determined by sex chromosomes can be dealt with in this context, but are ignored here to simplify this example.

Consider a population in which the receiving and signalling strategies are D and A respectively, and the distribution of quality genotypes is $G(\{D', A'\})$ for some $\{D', A'\} \in \mathcal{D} \times \mathcal{S}$. The signaller and receiver 'best response' maps, M_A and M_D are calculated as if the sender and receiver distributions of quality are $f(q) = g(q)$ and $f^\circ = g(q)$ respectively. In general, both M_A and M_D will be continuous in D, A, and g and therefore:

$$M : (\{D, A\}, \{D', A'\}) \mapsto (\{M_D(\{D, A\}), M_A(\{D, A\})\}, \{M_D(\{D, A\}), M_A(\{D, A\})\})$$

will also be continuous. Usually, it will be possible to apply a fixed point theorem to M Thus, as G is a surjection, the mapping induced on $\mathcal{D} \times \mathcal{S} \times \mathcal{G}$ by M will also have a fixed point. This fixed point is a signalling, receiving and quality genetic ESS.

The association of g with f and f° need not be identification as assumed above. Environmental and non-additive genetic variances can be included in the model by assuming either that g is the phenotypic distribution of q, or by including another continuous mapping from the space of genotype distribution $\mathcal{G}$ to the space of phenotype distributions, $\mathcal{P}$ (see Eshel (1996) for a useful way of viewing this relationship). This does not alter the model in any significant way, if it is assumed that relative costs of signalling and receiving are determined solely by phenotype quality as opposed to some interaction of phenotype and genotype quality. Note that in these cases, even if there is signalling and receiving which is error-free, receivers obtain information about phenotypic quality only. If they are interested in genetic quality as well, then they can only infer expected genotypic quality. In general, it will be reasonable to assume that these two are positively correlated.

3.3.2 Finite Number of Genotypes

A similar approach to the above can be applied to the case in which quality is dependent upon a finite number of quality genotypes, and so it is unnecessary to repeat the technicalities here. Assuming a finite number of genotypes also allows for more explicit genetics.

The only difficulty that arises in this case is that the results in chapter 2 rely on quality being continuously distributed. This is easily fixed by including continuous environmental variance in quality. Some technical problems arise if the receivers are interested in genetic quality, as it may not be an increasing function of phenotypic quality (though in haploid models expected genotypic quality will be increasing in phenotypic quality by Lemma B.1, if, for example, environmental variation is normally distributed with variance independent of genotype). This, whether it is made explicit or not, is a problem with all genetic models.

Another problem that may arise in explicit models of genetics is that we may not be able to physically calculate the ESS g for a given A and D, which leads to the problem of being unable to check that the ESS distributions are continuous in A and D. This may be solved by assuming that G is the mapping that sends g to its expected distribution in the next generation given A and D. Usually this mapping will be continuous in A, D and initial g. If generations are not assumed to be separate, i.e. cohorts may interbreed etc., then G could be replaced by an 'evolution function' $G(D, A, g, t)$. If G is assumed to satisfy time invariance:

$$G(D, A, g, t_1 + t_2) = G(D, A, G(D, A, g, t_1), t_2)$$

then an arbitrary time step may be chosen instead of generations. This method may also be used when the ESS distribution is discontinuous in A or D as, in general, the inter-generational change in genotype distribution will be continuous.

4 Theoretical Applications and Extensions

4.1 Error-Prone Signals

One of the motivations for Proposition 2.4 is that its set of conditions encompasses a wide range of models of error-prone signals. In this section, two types of error are considered: error in perception of a signal, and error in realization of a signal, where error in perception is defined as:

> the difference between the level of signal physically produced by the signaller, and the level perceived by the receiver;

and error in realization is defined as:

> the difference between the level of signal output by the signaller and the level which it 'intended', or the difference between the signal produced and the individual's mean level of signal in a given situation, or the difference between the signal produced and the mean level of signal performed by individuals of similar quality in the population.

The only difference between these two types of error, as far as the model is concerned, is whether the signaller pays direct costs for the error. Whilst this has little effect on the qualitative nature of signalling ESSs for given receiver strategies, it will be shown in section 5.4 that when interaction between receiver and signaller strategies are taken into acount, the results can be significantly affected by this distinction.

4.1.1 Additive Model of Error in Perception

First, consider the case where an individual actually advertising at level a is perceived at a level p with probability density $\epsilon(A, a, p)$, where it is assumed that e is absolutely continuous in a and continuous in A, and:

$$\int_{-\infty}^{\infty} p \cdot e(A,a,p) \cdot dp = a$$

The support shall of e with respect to p shall be denoted $\mathrm{supp}(e(A,a))$. (It is assumed that perceived levels of signal may lie outside the range of actual signals that are possible.)

If it is assumed that if the population strategy, A, is increasing in quality, the expected quality of a male is increasing in the level at which he is perceived, i.e.

$$\frac{d}{dp} \frac{\int_Q q \cdot e(A, A(q), p) f(q) \cdot dq}{\int_Q e(A, A(q), p) f(q) \cdot dq} \geq 0 \tag{4.1}$$

then the payoff to a signaller, given any reasonable receiver strategy, may be written in the form:

$$P(A,a,q) = V^q(A,q) \int_{-\infty}^{\infty} e(A,a,p) D(A,p) \cdot dp - C(A,a,q) \tag{4.2}$$

where $D(A,p)$ is continuous in A. increasing and bounded in p. Equation (4.1) is satisfied if, for instance, e satisfies the conditions on u in Lemma B.1.

Clearly, N (or $V^p N$) may be identified with the integral in equation (4.2). As integrals are absolutely continuous, Corollary C.3 may be applied to the model defined by equation (4.2) to show that an ESS exists. (An example showing how to calculate D is given in section 5.4.)

If the full weight of Proposition 2.4 is to be applied, then the only extra condition that $V^p N$ (i.e. the integral in equation (4.2)) must satisfy is the differential condition, equation (2.20). There are numerous conditions under which this is satisfied. One set of conditions is as follows:

$D(A,p)$ must be non-negative and for two disjoint measurable sets, $\mathcal{D}_1$, $\mathcal{D}_2$, for which:

$$\int_{\mathcal{D}_i \cap \left(\bigcap_{a \in \mathcal{A}} \mathrm{supp}(e(A,a))\right)} dp > 0, \qquad \forall A \in \mathcal{I} \tag{4.3}$$

where $D(A,\mathcal{D}_1) < D(A,\mathcal{D}_2)$. This condition may be interpreted as receivers prefering individuals perceived to be signalling high. The sets:

$$\mathcal{D}_i \cap \left(\bigcap_{a \in \mathcal{A}} \mathrm{supp}(e(A,a)) \right).$$

having non-zero measure means that the preference is actually seen. If e has support on the entire real line (such as if e is a normal distribution) then the integral conditions are trivially true.

Over and above this condition on receiver strategies, D, the error distribution needs to satisfy conditions which negate the possibility that an individual which bears a signal with low mean does not have a higher $V^p N$ than an individual which bears a signal with high mean, due to, for example, the signal with low mean having higher variance than the signal with high mean. Either of the following conditions is sufficient:

Condition 1: If for almost all A and a, whenever $p_1 < p_2$:

$$\frac{e_2(A,a,p_1)}{e(A,a,p_1)} < \frac{e_2(A,a,p_2)}{e(A,a,p_2)}$$

or, if e_2/e is absolutely continuous:

$$\frac{\partial}{\partial p}\left(\frac{e_2(A,a,p)}{e(A,a,p)}\right) > 0 \quad \text{a.e.}$$

This follows by Lemma B.1 of Appendix B. Recall that this condition also guarantees that equation (4.1) is satisfied.

Condition 2: If $e(A,a,p) = e(A,0,p-a)$ for all A, a and p. To see that this implies that the differential condition on N is satisfied, note that:

$$\begin{aligned}
\int_{-\infty}^{\infty} e(A,a_1+a_2,p)D(A,p)\cdot dp &= \int_{-\infty}^{\infty} e(A,a_1,p-a_2)D(A,p)\cdot dp \\
&= \int_{-\infty}^{\infty} e(A,a_1,p)D(A,p+a_2)\cdot dp \\
&> \int_{-\infty}^{\infty} e(A,a_1,p)D(A,p)\cdot dp
\end{aligned}$$

where the strictness of the last inequality follows from equation (4.3).

If e is the normal distribution with variance independent of a then it satisfies both of these conditions.

4.1.2 Error in Realization

If individuals of a certain quality attempt to signal at a level, $A(q)$, but do not always succeed, or if individuals do not signal at $A(q)$, but $A(q)$ is the mean level of signal of individuals of quality q, and individuals pay for the actual level of signal realized, then under what conditions do the results of Proposition 2.4 hold? Clearly, the error function should satisfy the conditions of the previous section as error in realization has the same effects on N as error in perception. The effect on the costs incurred is that individuals of quality q attempting to signal at a pay, on average:

$$\bar{C}(A,a,q) = \int_{-\infty}^{\infty} e(A,a,p)C(A,p,q)\cdot dp$$

where it is assumed that C is defined outside of $\mathcal{A} \times \mathcal{Q}$ if necessary and satisfies equations (2.21) and (2.22) for almost all a for all q. By arguments similar to those adduced in the previous section (with D replaced by C) it follows that $\bar{C}_2(A,a,q) > 0$ if e satisfies either Condition 1 or Condition 2. Similarly, as C_2/V satisfies equation (2.22) almost everywhere:

$$\frac{\partial}{\partial q}\left(\frac{\bar{C}_2(A,a,q)}{V(A,q)}\right) < 0$$

if e satisfies Condition 1 or Condition 2. Thus, Proposition 2.4 holds, with C replaced by $\bar{C}$.

Error in perception and realization may be easily combined in the one model; see section 5.4.

4.1.3 Effects of Signal Fidelity

This section considers the effects of large and small amounts of error upon signalling. $e(A,a,p,\sigma)$ represents a family of probability distributions parameterized by their standard deviations, σ. It is assumed that this family is continuous in σ under the $\mathcal{L}^1(-\infty,\infty)$ norm. For a given 'model' of female choice there will exist a related family, $D(A,p,\sigma)$, which are as in equation (4.2). It is assumed that $D(A,p,\sigma)$ is bounded above by a constant, β, which will hold for all biologically reasonable female strategies (cf. $N \in \mathcal{N}(9)$ in section 2.2).

Proposition 4.1 (Excessive Error in Perception) *Suppose that e is a family of normal distributions, then there exists σ_0 such that for all $\sigma \geq \sigma_0$ the only ESS of a model with error in perception (assuming error in realization is constant), is $A^*(q) = 0$ a.e.*

Proof: Let $A_R^\sigma(q)$ represent the best response to A given that the error in signalling has standard deviation σ. Now:

$$\begin{aligned} P_2(A,a,q,\sigma) &= \frac{V^q(q)}{\sigma^2}\int_{-\infty}^{\infty}(p-a)e(A,a,p,\sigma)D(A,p,\sigma)\cdot dp - C_1(A,a,q) \\ &\leq \frac{V^q(q)}{\sigma}\int_{0}^{\infty}\beta x\exp(-x^2/2)\cdot dx - C_1(A,a,q). \end{aligned}$$

Noting that the integral is independent of A we see that:

$$\lim_{\sigma\to\infty} P_2(A,a,q,\sigma) = -C_1(A,a,q).$$

As $\mathcal{Z}$ is compact, there exists σ_0 so that for all $\sigma \geq \sigma_0$ we have $P_2(A,a,q,\sigma) < 0$ for all $(A,a,q) \in \mathcal{Z}$. Thus A_R^σ is 0 a.e. for all $\sigma \geq \sigma_0$. Thus M_σ (defined in Proposition 2.4) sends $\mathcal{Y}$ to the equivalence class of functions containing $A(q) = a_{\min}$ for all $\sigma \geq \sigma_0$. □

Proposition 4.2 (Negligible Error in Perception) *Assume that:*

$$\lim_{\sigma\to 0} D(a_{\min},p,\sigma) = \begin{cases} d_0 & p < a_{\min} \\ d_1 & p = a_{\min} \\ d_2 & p > a_{\min} \end{cases}$$

where $d_2 > d_1$, then there exists $\sigma_1 > 0$ such that for all $\sigma \leq \sigma_1$, $A(q) = 0$ is not an ESS.

The condition on D in the above proposition is what we would expect in a model where female choice is of the form: sample males and choose the male perceived as advertising at the highest level.

Proof: As $\mathcal{Y}$ is compact and C/V^q is continuous, there exists continuous increasing $a(q) > 0$ and a constant c for which $C(A,a(q),q)/V^q(q) = c \leq (d_2 - d_1)/2$ for all A. Now, $\lim_{\sigma\to 0} P(a_{\min},a(q),q,\sigma)$ is equal to:

$$\lim_{\sigma\to 0} V^q(q)\int_{-\infty}^{\infty} e(a(q),a(q),p,\sigma)D(A,p,\sigma)\cdot dp - C(a(q),a(q),q) \qquad (4.4)$$

Upon noting the continuity of $D(A,a,p,\sigma)$ in p for all $\sigma > 0$ and the fact that:

$$\int_{|p-a|\geq s\sigma} e(A,a,p,\sigma)\cdot dp \leq \frac{1}{s^2}$$

it follows that the limit of the integral in equation (4.4) is d_2 and thus equation (4.4) is less than $V^q(q)(d_2+d_1)/2$. By continuity, for each q there exists σ_q so that:

$$P(a_{\min}, a(q), q, \sigma) > P(a_{\min}, a_{\min}, q, \sigma), \qquad \forall \sigma \leq \sigma_q.$$

Set $\sigma_1 = \sigma_{q_0}$ for some $q_0 \neq q_{\max}$. As $a(q)$ is increasing, we have $q \geq q_0$ implies $\sigma_q \geq \sigma_{q_0}$. Therefore, if $\sigma \leq \sigma_1$, 0 is not the best response to $A(q) = 0$ for $q \in [q_0, q_{\max}]$ and thus $A(q) = 0$ is not an ESS. □

Under slightly different conditions it is possible to be even more precise. Consider a set of additive models of error-prone signalling parameterized by their error standard deviation. Let $P_\sigma(A, a, q)$ represent the payoff to an individual of quality q signalling with mean a in a population playing $A(q)$, where σ is the amount of error in signalling. No assumptions are made about the proportion of error which is due to error in perception and the proportion due to error in realization. $P_0(A,a,q)$ represents the payoff in the equivalent error free signalling model. We have the following proposition.

Proposition 4.3 (Continuity of ESSs) *Denote the set of ESSs to P_σ by $\mathcal{E}_\sigma$. Assume that P_σ satisfies the conditions of Corollary C.3 for all $\sigma \in [\sigma_1, \sigma_2] \overset{def}{=} \mathcal{W}$, and that $P_\sigma(A,a,q)$ is continuous in σ for all $(A,a,q) \in \mathcal{I} \times \mathcal{A} \times \mathcal{Q}$. Then for all $\sigma_\ell \in \mathcal{W}$:*

$$\lim_{\sigma \to \sigma_\ell} \mathcal{E}_\sigma = \mathcal{E}_{\sigma_\ell}$$

That is, for all $\epsilon > 0$ there exists $\delta > 0$ such that:

$$0 < | \sigma_\ell - \sigma | < \delta$$

implies that for each $A_\sigma \in \mathcal{E}_\sigma$ there exists $A_\ell \in \mathcal{E}_{\sigma_\ell}$ such that:

$$\| A_\ell - A_\sigma \| \overset{def}{=} \int_{\mathcal{Q}} | A_\ell - A_\sigma | f(q) \cdot dq < \epsilon$$

In particular, this Proposition 4.3 confirms Johnstone's (1994) simulation results which suggest that as error in signalling goes to zero the ESSs limit to the ESS(s) of the corresponding error-free signalling model. It should be noted that the above result does not guarantee that card($\mathcal{E}_\sigma$) is constant in σ.

There is no reason why σ cannot be interpreted as an arbitrary free paramater, instead of as the amount of error in a given signalling system. Thus, this proposition may be used to analyse the ESSs of games that are small deformations or 'homotopies' of games for which the ESSs are known. For example, games that satisfy the conditions of Proposition 2.1 have a unique signalling ESS. One of the conditions of Proposition 2.1 is that C is independent of A. Proposition 4.3 then confirm that a game in which C is only 'slightly' dependent upon A will have ESSs that are approximated by the unique ESS of a game in which C is independent of A. Another application of this result is given in section 6.1.4.

Proof: Define $P_\sigma(A, B)$ by:

$$P_\sigma(A, B) \overset{\text{def}}{=} \int_Q (P_\sigma(A, B(q), q) + C(A, a_{\min}, q)) f(q) \cdot dq$$

and set $\Phi_\sigma(A) = P_\sigma(A, A) - P_\sigma(A, A_R)$ where A_R is the unique best response derived in the proof of Proposition 2.4. Clearly $\Phi_\sigma(A)$ is continuous in both σ and A. Moreover, $\Phi_\sigma(A) = 0$ if and only if A is its own best response. By uniqueness of best responses this implies that $\Phi_\sigma(A) = 0$ if and only if $A \in \mathcal{E}_\sigma$.

Define $\mathcal{O}_\epsilon$ by:

$$\mathcal{O}_\epsilon \overset{\text{def}}{=} \left\{ A \in I;\ \inf_{A^* \in \mathcal{E}_{\sigma_\ell}} \| A^* - A \| < \epsilon \right\}$$

As $\mathcal{I} - \mathcal{O}_\epsilon$ is compact, and all the zeroes of Φ_{σ_ℓ} are contained in $\mathcal{O}_\epsilon$, there exists $b < 0$ such that $\Phi_{\sigma_\ell}(A) < b$ for all $A \in \mathcal{I} - \mathcal{O}_{\sigma_\ell}$ (by Theorem 6.4 in Munkres 1975), as Φ_{σ_ℓ} is continuous in A.

Now, consider the mapping $\Psi : \sigma \mapsto \Phi_\sigma$. As Φ_σ is continuous in A and σ, Ψ is a continuous mapping of $\mathcal{W}$ into the space of continuous functions from $\mathcal{I}$ to $\mathbb{R}$ under the 'sup' metric (see below and Munkres 1975, p267-8).

As $\mathcal{W}$ is compact Theorem 7.3 of Munkres (1975) implies that there exists a $\delta > 0$ such that:

$$0 < | \sigma - \sigma_\ell | < \delta \Longrightarrow \sup_{A \in \mathcal{I}} | \Phi_\sigma(A) - \Phi_{\sigma_\ell}(A) | < | b |$$

In particular if $| \sigma - \sigma_\ell | < \delta$ and $\Phi_\sigma(A) = 0$ then $A \in \mathcal{O}_\epsilon$, which in turn implies that $\mathcal{E}_\sigma \subseteq \mathcal{O}_\epsilon$ which is the required result. □

4.2 Bounded Advertising

In section 6.3.1 it is shown that under some conditions, high quality individuals may not be able to advertise highly enough to distinguish themselves from individuals of lower quality as the solution to the first order differential equation that must be satisfied by an ESS asymptotes at some value of q. The assumption that an individual can always advertise at a marginally higher level, used in the proof of Lemma 2.3, no longer holds. An ESS exists in this situation, with all the individuals above a certain quality advertising at $a = \infty$, the cost associated with this being $\lim_{a \to \infty} C(a, q)$, which must exist as it may be shown that if the solution asymptotes at q', $C(a, q)$ is bounded for $q \geq q'$, and $C(a, q)$ is monotonic.

The following proposition takes a slightly different approach to the same problem. It is assumed that there is a level above which no individual can advertise, which is equivalent to the first order condition asymptoting via a homeomorphism $[a_{\min}, a_{\max}] \to [a_{\min}, \infty]$. Pigmentation could be a possible example of such a signal; after a certain density of pigment has been deposited over the entire animal's integument, there is nothing left to colour and, thus, there is a maximum possible signal.

For clarity of exposition, it is assumed that receivers use a pool-comparison method (see sections 2.2 and 5) and select the signaller advertising at the highest level. The proposition is easily generalized, but this requires extra opaque conditions on N so that it satisfies 'common sense'; this is left to the reader.

By noting equation (6.5) and the discussion of section 6.1, it will become clear that the result below is applicable to the WOA with continuous random rewards, as well as the OICG. Taking the limit:

$$\frac{\partial}{\partial q}\left(\frac{C_1(a,q)}{V(q)}\right) \to 0$$

it is easy to check that the results obtained below are concurrent with Bishop and Canning's (1978) Time-Limited War of Attrition.

Proposition 4.4 (Bounded Signals) *Let $q_{\max}-q_{\min} < \infty$, $a_{\max} < \infty$, and F be a strictly increasing absolutely continuous function of q. Suppose $N \in \mathcal{N}(1-10)$, that V and C are independent of A, that $C(a,q)$ is absolutely continuous in a, and that the partial derivative of $C_1(a,q)/V(q)$ with respect to q is continuous on $\mathcal{A} \times \mathcal{Q}$. Further suppose that:*

$$\begin{aligned} C_1(a,q) &> 0, \quad \text{for a.a. } (a,q) \in \mathcal{A} \times \mathcal{Q} \\ \frac{\partial}{\partial q}\left(\frac{C_1(a,q)}{V(q)}\right) &< 0, \quad \text{for all } (a,q) \in \mathcal{A} \times \mathcal{Q} \end{aligned} \tag{4.5}$$

Then there exists a unique increasing signalling ESS, $A^*(q)$, to the game defined by equation (2.1).

Proof: First note that by Lemma 2.3 that any ESS must be strictly increasing on $[a_{\min}, a_{\max})$. Denote by A_{sol} the solution to the differential equation:

$$\frac{dA_{sol}(q)}{dq} = \frac{V(q)N'(A_{sol}, A_{sol}(q))}{C_1(A_{sol}(q), q)} \quad a.e.$$

with the intitial condition $A_{sol}(q_{\min}) = a_{\min}$, where $N(A_{sol}, A_{sol}(q))$ is a known function as $N \in \mathcal{N}(6)$. $A_{sol}(q)$ is unique on its domain of existence by Propositions A.1 and A.3.

There are two possibilities:

Case 1: If $A_{sol} \leq a_{\max}$ for all $q \in \mathcal{Q}$, then the arguments of Proposition 2.1 show that A_{sol} is the unique ESS.

Case 2: If, on the other hand:

$$\lim_{q \uparrow q_a} A_{sol}(q) = a_{\max}$$

it can be shown that the only possible ESS for males is of the form:

$$A^*(q) = \begin{cases} A_{sol}(q) & \forall q \in [q_{\min}, q_c) \\ A_{sol}(q_c) \text{ or } a_{\max} & \text{if } q = q_c \\ a_{\max} & \forall q \in (q_c, q_{\max}] \end{cases}$$

where $q_c < q_a$. It will be shown that either q_c is unique, or $q_c < q_{\min}$ (i.e. $A^*(q) = a_{\max}$ for all $q \in \mathcal{Q}$).

To see the above claim, first note Lemma 2.3 and the proof of Proposition 2.1 shows that an ESS must be of the form (almost everywhere):

$$A_t(q) = \begin{cases} A_{sol}(q) & \forall q \in [q_{\min}, q_t) \\ a_{\max} & \forall q \in (q_t, q_{\max}] \end{cases}$$

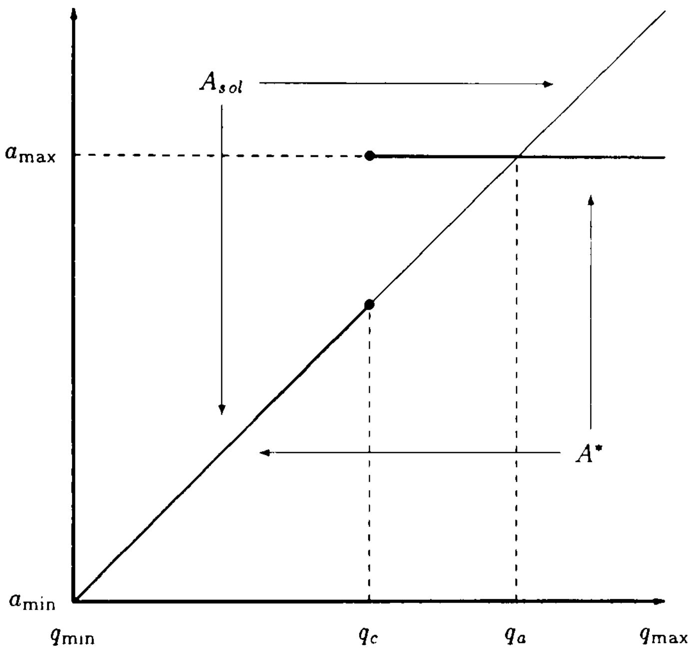

Figure 4: *Qualitative comparison of ESS to unbounded and bounded signalling games. The ESS to the unbounded game (i.e. Proposition 2.1), A_{sol}, is represented by the 45° line, whilst the ESS to the bounded signalling game (i.e. Proposition 4.4), A^*, is given by the thicker portion of the 45° line and the thick horizontal line. Note that q_c is always strictly less than q_a, and that $a_{\max}$ in the diagram is the bound on advertising in Propsition 4.4, which should not be confused with the upper bound of $\mathcal{A}$ in Proposition 2.1 of the same name.*

where $q_t \in (-\infty, q_a]$. The payoff to a male of quality q advertising at level a in a population playing A_t is:

$$P(A_t, a, q) = \begin{cases} V(q)N(A_t, A_t^{-1}(a)) - C(a, q) & \text{if } a < A_{sol}(q_t) \\ V(q)N(A_t, q_t) - C(a, q) & \text{if } A_{sol}(q_t) \leq a < a_{\max} \\ V(q)N(A_t, a_{\max}) - C(a_{\max}, q) & \text{if } a = a_{\max} \end{cases}.$$

Note that the payoff to a male advertising at $A_{sol}(q_t)$ is always greater than the payoff to a male for which $a \in (A_{sol}(q_t), a_{\max})$. An ESS must satisfy:

$$N(A_t, a_{\max}) - N(A_t, A_{sol}(q)) - \frac{C(a_{\max}, q) - C(A_{sol}(q), q)}{V(q)} \geq 0 \qquad (4.6)$$

for all $q > q_t$ and must be less than 0 for all $q < q_t$. Upon noting that equation (4.6) is strictly increasing and continuous in q the problem reduces to finding q_t so that the equation is equal to zero for $q = q_t$. Now:

$$N(A_t, a_{\max}) - N(A_t, A_{sol}(q_t)) - \frac{C(a_{\max}, q_t) - C(A_{sol}(q_t), q_t)}{V(q_t)}$$

is a strictly increasing function of $q_t \geq q_{\min}$ as $N \in \mathcal{N}(10)$, $N(A_t, a_{\max})$ is an increasing function of the parameter t, and the derivative:

$$\frac{d}{dq_t}\left(-N(A_t, A_{sol}(q_t)) - \frac{C(a_{\max}, q_t) - C(A_{sol}(q_t), q_t)}{V(q_t)}\right) > 0 \qquad (4.7)$$

To see this last claim, note that the left hand side of equation (4.7) may be expanded:

$$N(A_t, A_{sol}(q_t)) + \frac{C_1(A_{sol}(q_t), q_t)}{V(q_t)} A'_{sol}(q_t) - \frac{\partial}{\partial q}\left(\frac{C(a_{\max}, q) - C(A_{sol}(q_t), q)}{V(q)}\right)\Bigg|_{q=q_t}$$

The first two terms of the above equation sum to zero by the definition of A_{sol}. The last term is is equal to (almost everywhere):

$$-\int_{A_{sol}(q_t)}^{a_{\max}} \frac{\partial}{\partial q_t}\left(\frac{C_1(a, q_t)}{V(q_t)}\right) \cdot da$$

and by equation (4.5), is positive. Thus, the male ESS is $A^*(q) = a_{\max}$ for all q if:

$$V(q_{\min})N(A_{a_{\min}}, a_{\max}) - C(a_{\max}, q_{\min}) > 0.$$

If the above equation is not true, then the Intermediate Value Theorem implies that there exists a $q_c \in [q_{\min}, q_a)$ for which A_c is an ESS, and this ESS is unique. □

A population in which a range of individuals signal at the maximum possible level would be prone to the invasion of a second signal, as the higher quality individuals signalling at $a = \infty$ would be able to increase their fitness by distinguishing themselves from the lower quality individuals signalling at $a = \infty$. If this second signal was also cheap and bounded, there would remain the possibility of the invasion of a third signal, and so on. The strategic handicap principle asserts that a population signalling strategy (which relates signal level to an individuals 'quality') is long term evolutionarily stable only if for each individual the marginal cost of increasing the level of signal (or signals) would outweigh the marginal benefits that could be gained by doing so. Thus, depending on the particular details of the situation, the evolutionary consequences of such a process of successive invasion of signals might be a stable collection of a number of individually bounded and cheap signals which are collectively expensive, or perhaps a potentially unbounded signal together with a number of cheap and bounded signals.

4.3 Free Signals

4.3.1 Irregular Lower Bounds

In chapter 2 it was assumed that all individuals minimized their costs or maximized their 'survival' at $a = a_{\min}$ or that $a_{\min}$ was a natural lower bound to the signal. Such assumptions may not always be tenable and, as the following partial analysis will show, are not innocuous. The following analysis of the more general situation is given in the framework of the multiplicative partitioning of fitness (section 2.3). It can, of course, be related to the additive partition by exponentiation.

Suppose that $a_{\min} = -\infty$, and $S(A, a, q)$ is maximized for each q at $A^\circ(A, q)$. Further suppose that $S_2(A, a, q) < 0$ for all $a > A^\circ(A, q)$ and $S_2(A, a, q) > 0$ for all $a < A^\circ(A, q)$.

We know from Lemma 2.1 that any PBR must be increasing if certain conditions are satisfied. This result does not necessarily hold in the more general framework outlined here, as the second order condition on S will not hold if, for instance, $A^\circ(A, q)$ is strictly decreasing.

Problems even occur when $A^\circ(A, q) > A^\circ(A, q_{\min})$. If this is the case then 'best responses', and hence ESSs, may not be given by $M(A)$ (the 'best response' defined in the proof of Proposition 2.3), as $M(A)$ may cross $A^\circ(A, q)$ and hence wander into regions in which $S_2(A, a, q) > 0$, which results in Lemma 2.4 no longer being valid. This means that there is no guarantee that $M(A)$ is a PNE. In fact, below $A^\circ(A, q)$, $M(A)$ is decreasing; Lemma 2.3 then shows that it cannot be a PNE. ESSs still exist in this case, however a complete analysis of the situation is perhaps only of technical interest.

It is not the purpose of this section to analyse the relaxing of the common lower bound condition; however, one special case is particularly interesting, as it illustrates that strategic signals may be 'free' in the sense that the ESS signalling strategy is also the strategy that maximizes individual survival.

4.3.2 Conditions for the Existence of Free Signals

Suppose that $A(q) = A^\circ(A, q)$, that is the population plays a strategy in which individuals maximize their 'survival' Can this ever be an ESS?

Suppose that $A(q)$ is strictly increasing. If S is smooth in a at $A^\circ(A, q)$ then perusal of the form of $P_2(A, a, q)$ shows that $P_2 \leq 0$ is not possible close to $A^\circ(A, q)$ as $S_2(A, a, q)$ is arbitrarily small, close to $A^\circ(A, q)$ for all q, and on the same region $N_2(A, a)$ is bounded away from zero for all but $q_{\min}$ and $q_{\max}$. Thus, if $A(q) = A^\circ(A, q)$ is to be an ESS, and N is to satisfy the 'reasonable' conditions of section 2.2 or Proposition 2.4, then $S(A, a, q)$ cannot be differentiable in a at its maximum.

The reasonableness of free signals, at least in this model, then depends on two factors:

1. Whether or not it is reasonable that the level of signal that is produced at an individual's optimum level of survival is increasing in individual quality.
2. Whether or not it is reasonable for S_2 to be discontinuous at its optimum.

These two conditions do not guarantee that a signal will be free at equilibrium, in the modelling framework used here. They are merely necessary conditions.

A signal will be free in the multiplicative model of section 2.3 if the N arising from the receivers' best response to A satisfies:

$$\frac{N_2(A, A(q))}{N(A, A(q))} < \frac{-S_2(A, A(q), q)}{S(A, A(q), q)}$$

That is, the signal will be free if the marginal benefit of increasing the signal above the level which is obtained at the optimum survival strategy is less than the cost of increasing the signal by deviating from the optimal survival strategy. Whether or not this condition is satisfied depends on numerous other conditions.

4.3.3 Reasonableness of Separating Signals at Survival Optimum

It is easy to see that the first factor is easily satisfied. For example, suppose that q represented a male's current level of parasitisation, a quality that may be of interest to females because of a correlation with the male's immune system or his current ability to forage. Suppose that the signal was an underwing speculum. The colour of this speculum is produced by the deposition of carotenoids. The size and/or intensity of this patch is dependent upon the amount of a certain pigmenting compound in the male's diet that are excess to his other physiological requirements and which are available for deposition. It is plausible that, as the speculum is hidden, there are no extrinsic costs to the coloured patch (e.g. due to predation).

Now consider the situation in which all males forage optimally, in terms of their survival. There are multifarous ways in which the amount of the pigmenting compound that can be deposited during the moult may differ between individuals of different qualities, e.g.:

1. Individuals of different qualities may forage in different areas or manners; an individual of low quality might forage in areas which are less than optimal because relatively high competition or predation costs due to their inferior health might exclude them from foraging on better areas.
2. The efficiency of deposition of the pigmenting compound may be decreased by parasitic infection.
3. The pigmenting compound might be important to the male's immune response. If the individual is infested or infected, then less of the compound would be available for deposition as more of it would be used by the immune system. (From the strategic perspective, this assumes that the marginal cost of diverting resources from the immune system is not outweighed by the mating benefit of the increased signal.)

Thus, it is clear that individuals maximizing their survival may end up with different signals, and that this difference is correlated with some given quality.

4.3.4 Reasonableness of S_2 being Discontinuous at Optimum

A priori, this does not seem reasonable. However, it can arise naturally when the signallers are related. See section 7.4 for more details.

4.3.5 Conditions for Cheap Signals

Deeper inspection of the analysis which shows that S_2 must be discontinuous for free signals to be ESSs, shows that cheap, but not totally free, signals do not need to satisfy this condition. It is necessary that the marginal cost of increasing a signal, S_2, is more than the marginal benefit, N_2, if a signalling system is to be stable against invasion by individuals which signal marginally higher than the norm. If S is smooth and $N_2 > 0$ then this cannot be the case at S's optimum. However, if S_{22} is much greater than N_{22}, the ESS may be quite near this optimum.

4.4 Signal Dependent Quality and Predator Prey Signalling

Three papers (Nur & Hasson 1984; Vega-Redondo & Hasson 1993; Yachi 1995) have considered strategic signals in the context of predator prey interactions, and there is some empirical evidence to support the claim that certain behaviours are honest signals of a prey individual's condition to predators (FitzGibbon & Fanshawe 1988). The two models that have been solved by analytical methods (Vega-Redondo & Hasson 1993; Yachi 1995) have assumed that the quality of prey is discretely distributed. The purpose of this section is to show how the arguments of chapter 2 can be used to solve continuous analogues of these models.

Predator-prey signalling models differ from other models of strategic signalling that have appeared in the literature in that the signal not only affects the fitness of the signaller, but also affects the quality of interest to the receiver. By stotting or allowing a predator make a close approach before fleeing, a member of the prey species reduces its chance of survival if it is chased. Similar effects could be expected in the case of exhausting signals of fighting ability (note the circumstances described in Clutton-Brock & Albon (1979)), or in the case of signals of parental ability that reduce the signallers chance of surviving the period of offspring rearing, or reduce their foraging efficiency.

4.4.1 Continuous Formulation of Predator-Prey Models

Nur & Hasson (1984), Vega-Redondo & Hasson (1993), and Yachi (1995) all utilize the same basic prey fitness equation:

$$P(A, a, q) = H(A, a) + E(A, a, q)(1 - H(A, a))$$

where H is the probability that an individual is not chased and E is the probability that if it is chased it will escape. Clearly, we should expect that $E_2 < 0$ and $E_{23} > 0$, i.e. the higher an individual signals the more likely it is to be caught if it is chased, and this marginal increase of escaping is increasing in individual quality. Assume further that H satisfies the conditions on N in either Proposition 2.1 or Proposition 2.4, and that the base chance of escaping is increasing in individual quality, i.e. $E_3(A, a_{\min}, q) \geq 0$. After setting $V = 1$ and $N = H$ and $C = -E(1 - H)$, simple calculations show that the basic conditions for the existence of a signalling ESS are satisfied.

4.4.2 ESSs are Potentially Unreasonable

As pointed out by the above authors of predator-prey models, consideration of the predator strategy may mean that the signalling ESS obtained is spurious when viewed in the full context of predator-prey interaction. This is because predators are not interested in the prey's quality *per se*, but in the ease with which it may be caught, i.e. E. There is no guarantee that E is increasing with q once the effects of signalling have been taken into account, as can be seen from the following calculation.

To simplify the following analysis, restrict the analysis to the case in which $H \in \mathcal{N}(1-5, 7-10)$. In particular, this guarantees that any ESS is absolutely continuous. For $E(A, A(q), q)$ to be consistent with the predators strategy giving rise to $H(A, a)$ being increasing in a, it should satisfy:

$$\frac{dE}{dq} = E_2(A, A(q), q)A'(q) + E_3(A, A(q), q) \geq 0$$

After replacing $A'(q)$ with the right hand side of the equilibrium condition, the above condition reduces to:

$$E_3(A, A(q), q) + \frac{(E(A, A(q), q) - 1)H_2(A, A(q))}{1 - H(A, A(q))} \geq 0$$

The left summand is positive, and the right summand is negative. Whether a potential ESS, $A(q)$, is reasonable when predators' decisions are taken into account is then dependent upon the relative values of the summands.

4.4.3 Reformulation of Predator-Prey Signalling Model

The uncertainty about whether or not the preys' signalling ESS obtained in the standard analysis of chapter 2 is reasonable from the predator's perspective disappears if the model is approached from a slightly different perspective. The idea is to rule out H's and A's that cannot arise from an optimal predator strategy, without having to calculate the predator strategy explicitly.

The predators' response to a population strategy signalling strategy a in a population which signals at $A(q)$, and hence $H(A, a)$, should not be dependent on the inferred quality $A^{-1}(a)$ of the signalling prey, but on the expected value of $E(A, a, A^{-1}(a))$. Therefore, if $A(q)$ is strictly increasing, but $E(A, A(q), q)$ is not strictly increasing, then $A(q)$ cannot be a PNE. For if $E(A, A(q_2), q_2) \leq E(A, A(q_1), q_1)$ for some $q_1 < q_2$ then $H(A, A(q_2)) \leq H(A, A(q_1))$ and thus individuals of quality q_2 can improve their fitness by signalling at the lower level, $A(q_1)$, as $E \leq 1$ and $E_2 < 0$.

Thus, although $H(A, a)$ is not necessarily an increasing function of a, we can restrict our attention to the subset of increasing signalling strategies for which $H(A, A(q))$ is increasing for all $q \in \mathcal{Q}$. This set will be denoted by $\mathcal{H}$.

To proceed further, two assumptions will be made. These are:

1. There is no error in the realization of the signal nor is there any error in perception of the signal.

2. Signals not normally seen in the population are treated by predators as if they were made by individuals whose quality is the same as the quality of individuals signalling at the highest level in the population which is lower than the signal not normally seen in the population. Signals lower than any normally seen in the population are considered to have come from individuals of the lowest possible quality. (See $\mathcal{N}(2)$ in section 2.2.3 for mathematical formulation of similar assumptions.)

These assumptions will be referred to by number in the following arguments. Neither of the assumptions are necessary conditions; an equivalent analysis for error-prone signals is possible, for instance. Formal proofs of the assertions below are not given explicitly, but may be constructed in a manner similar to the proofs of the lemmas in section 2.2.

Under these assumptions, an ESS, $A^*(q)$, cannot be discontinuous. To see this, note that as E is strictly decreasing in a, a predator playing its optimal response to a strategy $A(q)$ should be at least as likely to pursue an individual which signals at a level not seen in the population, as an individual which signals at the highest level normally seen in the population that is lower than the unusual signal. Mathematically, H is decreasing over any interval for which $A^{-1}(a)$ does not exist. Moreover, if A is discontinuous at q' then as $E_2 < 0$:

$$\lim_{q \uparrow q'} H(A, A(q)) > \lim_{q \downarrow q'} H(A, A(q))$$

Thus, as $E < 1$, signallers of quality $(q', q' + \delta)$, some suitably small δ, can increase their fitness by signalling at $\lim_{q \uparrow q'} A(q)$ (cf. Lemma 2.4). Thus if A is a PNE, it must be continuous.

Similar arguments show that $A(q_{\min}) = a_{\min}$ (cf. Lemma 2.6).

To simplify the rest of the argument, assume that $E(A, a, q)$ is independent of A (an assumption made in all three papers cited in this section). In this case, the set of A for which $H(A, A(q))$ is increasing in q, is identical with the set of A for which $E(A, A(q), q)$ is increasing in q. Moreover, this set is homeomorphic to a convex set, by noting that if $A \in \mathcal{H}$ and $B \in \mathcal{H}$, then the function T defined implicitly by:

$$tE(A, A(q), q) + (1 - t)E(A, B(q), q) = E(A, T(q), q)$$

is also in $\mathcal{H}$.

After changing variables $H(A, \epsilon) = H(A, A(q))$, where $e = E(A, A(q), q)$, we see that at a PNE:

$$H_2(A, \epsilon) + (1 - H(A, e) - eH_2(A, e) = 0$$

Noting that H decreases as ϵ increases, this may be integrated to give:

$$\frac{1 - H(A, a_{\min})}{1 - H(A, e)} = \frac{1 - E(A, a_{\min}, q_{\min})}{1 - \epsilon}$$

Define $M(A)$ implicitly by:

$$\frac{1 - H(A, a_{\min})}{1 - H(A, A(q))} = \frac{1 - E(A, a_{\min}, q_{\min})}{1 - E(A, M(A)(q), q)}$$

M will be continuous in A. A fixed point of M is an ESS. This ESS is compatible with a predator strategy of preferring to pursue prey that signal at a low intensity. The model can be extended to incorporate feedback effects between prey and predator strategies by the methods outlined in chapter 3 and illustrated in chapter 5.

5 Example—Pool Comparison Sexual Selection

So far, the modelling in this paper has been extremely abstract. In particular, there has only been a sketch of how to incorporate the coevolution of receiver/signaller strategies and how to include genetics. One of the principal conclusions of this paper is that we should not need to re-check each specific model of female choice or male cost function etc. However, it is always enlightening to solve examples explicitly.

In sections 5.2 to 5.4 a number of models of sexual selection are solved. They are all of based on females using a pool-comparison strategy. Sticking to one particular female discrimination strategy allows comparison of the various assumptions that can be made. To illustrate the effects of female discrimination strategies on male advertising, similar models are solved with a different female discrimination strategy in section 5.5.

5.1 Female Pool Comparison Strategy

The pool-comparison or 'best of n' strategy is a commonly assumed strategy in models of sexual selection (Real 1990; Seger 1985; O'Donald 1980; Janetos 1980). Females are assumed to choose the 'best' individual from a random sample of males from the population. The assumption of random sample of males is probably unrealistic. The effects of non-random sampling of males, non-random association of males (e.g. Dugatkin & Sargent 1994; Metcalfe & Thomson 1995) or copying of female choice (Shuster & Wade 1991; Pruett-Jones 1992; Dugatkin & Godin 1992,1993; Kirkpatrick & Dugatkin 1994) will, in general, be to increase the variance in male mating success (Wade & Pruett-Jones 1990).

5.1.1 Optimal Female Strategy

For simplicity, assume that females may choose from a non-integer number of males. This makes some sense if we view n not as the actual number of males sampled, but as more abstract representation of the intensity of female discrimination. Females are assumed to vary in 'quality', $q \in Q$, with cumulative distribution function $F^{\circ}(q)$. The cost in fitness to a female sampling from n males is denoted $K(A, n, q)$ and it is assumed that the fitness of a female mating with a male of quality q_m is given by $R(q_m)$. Total female fitness is assumed to be $R - K$.

Proposition 5.1 *Assume that the cost of sampling n males, $K(A, n, q)$ satisfies, $K_2 \geq 0$, $K_{22} > 0$, and $K_{23} \leq 0$ (with equality only possible at $n = 1$ for K_2 and K_{23}). If males are continuously distributed, females can distinguish between* *males of each quality, and female reproductive fitness, $R(A, q)$, is a strictly increasing function of mate quality, then there exists a unique optimal level of discrimination for females of each quality. Moreover, amongst discriminating females this level is strictly increasing in female quality.*

Proof: Let $x(A, a)$ represent the post selection cumulative distribution function of males perceived to be advertising at level a. Denote by $E(R, x)$ the expectation value of fitness of a female mating with a male who is perceived to be advertising at a level given implicitly by $x(A, a)$.

The payoff to a female is given by:

$$\int_0^1 E(R, x) n x^{n-1} \cdot dx - K(A, n, q).$$

Let $I(A, n)$ denote the integral in the above equation. If $E(R, x)$ is increasing in x then:

$$I_2(A, n) = \int_0^1 E(R, x)(1 + n \ln x) x^{n-1} \cdot dx.$$

Noting that $E_2(R, x) \geq 0$, that:

$$\int_0^1 (1 + n \ln x) x^{n-1} \cdot dx = 0$$

and that $1 + n \ln x$ is negative on $(0, \exp(-1/n))$ and positive on $(\exp(-1/n), 1)$, we see that $I_2(A, n) \geq 0$.

Next consider:

$$I_{22}(A, n) = \int_0^1 E(R, x)(2 \ln x + n \ln^2 x) x^{n-1} \cdot dx.$$

Upon noting that $E_2(R, x) \geq 0$, that:

$$\int_0^1 (2 \ln x + n \ln^2 x) x^{n-1} \cdot dx = \frac{-4n - 2}{n^2 (n+1)^2}$$

and that $2 + n \ln x$ is negative on $(0, \exp(-2/n))$ and positive on $(\exp(-2/n), 1)$ we see that $I_{22}(A, n) \leq 0$.

Given this, $I_{22}(n) - K_{22}(A, n, q) < 0$ and thus there can exist at most one critical value of the female payoff for each A and q, which, if it exists, must be a maximum. Now $I(A, n)$ is bounded above by $R(q_{\max})$ and thus:

$$\lim_{n \to \infty} I(A, n) - K(A, n, q) = -\infty$$

which implies that a maximum exists. If $I_2(A, 1) - K_2(A, 1, q) \leq 0$ then the maximum is for females of quality q is to choose from only one male, i.e. for females not to discriminate. Otherwise, the optimal female strategy is to be discriminating.

Then, as $K_{23} < 0$ except possibly at $n = 1$, the cumulative distribution of optimal female strategies is:

$$\begin{aligned} D(A, 1) &= \int_{q_{\min}}^{\{q, I_2(A,1) < K_2(A,1,q)\}} F_2^{\circ} \cdot dq \\ D_2(A, n) &= F_2^{\circ}(A, q_n), \quad \text{where } q_n \text{ uniquely satisfies } I_2(A, n) = K_2(A, n, q) \end{aligned}$$

□

Note that, as $K_{22} < 0$, D is continuous in n. Similarly, if both $E(R, x)$ and K are continuous in A, then so is D.

The case $K_{23} \leq 0$ may be dealt with if the theory of integration used allows points to have non-zero measure.

It should be noted that the above analysis does not imply that receivers have higher fitness at a signalling equilibrium than at a non-signalling equilibrium, as the cost of a particular strategy to females is dependent upon A. For example, at a signalling equilibrium it may be the case that males are harder to find because of higher mortality than at a non-signalling equilibrium, so even females that are willing to mate with the first male that they find will suffer a reduction in fitness relative to the case in which males do not signal (see example in Grafen 1990a, p482-3).

5.1.2 Discrete Model

The arguments of Proposition 5.1 may also be used to provide a proof of what the best possible integer strategies are. Instead of the assumptions on $K(n)$ made previously, assume:

$$\frac{K(n) - K(n-1)}{K(n+1) - K(n)} < 1 \quad \text{for all integer } n \geq 2 \tag{5.1}$$

This is the discrete way of saying that the marginal cost of choosing males is increasing. As $I(n)$ is bounded above by $R(q_{\max})$:

$$\lim_{n \to \infty} I(n) - K(n) = -\infty$$

and thus a maximum is obtained. The previous proposition gives:

$$\frac{I(n+1) - I(n)}{I(n+2) - I(n+1)} \geq 1$$

and together with equation (5.1) implies that if n is a maximum then $n + m$ cannot be a maximum for $m > 1$. If there exists n for which $I(n+1) - I(n) = K(n+1) - K(n)$ then both n and $n+1$ are the only maxima; if no such n exists then the maximum is unique.

Any function that satisfies the continuous conditions also satisfies the discrete conditions for integer values. Similarly, any function that satisfies the discrete condition may be extended to a continuous function that satisfies the continuous conditions for all germane real n. Moreover, if n is the best strategy in the continuous model, then the best strategy in the integer model is $[n]$ and/or $[n+1]$, where $[m]$ denotes the integer part of m. If n and $n+1$ are best strategies in the integer model, then the best strategy of any continuous extension must lie within $(n, n+1)$. If the best strategy to an integer model is singular, n, then the best strategy of any continuous extension must lie within $(n-1, n+1)$.

Now, suppose K satisfies the conditions of Proposition 5.1 and further suppose that F° is continuous. As $K_{23}(A, n, q) < 0$ for all $n > 1$ and $I(A, n)$ is independent of q, it follows that only a set of measure zero of females have their reproductive success maximized at both n and $n+1$. This gives rise to a discrete cumulative probability distribution, $D(A,n)$ of the number of females who sample from a pool of n males, which satisfies:

$$D(A,n) = \sum_{i=1}^{n} D'(A,i), \qquad \lim_{n\to\infty} D(A,n) = 1$$

where $D'(A,n)$ is the proportion of females whose optimal strategy, given the male strategy A, is to sample n males. The quality of females who sample from n is less than the quality of females who sample from $n+1$.

It should be noted that F° being continuous in q, implies that $D'(A,n)$ and $D(A,n)$ are continuous in n. Further, D is continuous in A as K and I are continuous in A.

Results similar to those that are derived in the examples below may be derived for the discrete model of choice, simply by replacing the integral over n by summation.

5.1.3 Why Things Look Different from a Male Perspective and the Definition of $\Lambda(n)$

Females can expect to choose from n males with probability density $D'(n)$ (or probability D' in the discrete case). However, this is not the probability density that an arbitrary male in the population encounters a female which is sampling n males. The correct probability density in this case would be proportional to $nD'(n)$. This is because in sampling with replacement, the frequency at which an individual appears in a sample of a given size is determined by:

$$\text{Frequency of Being Sampled} = \frac{\text{Nō of Samples} \times \text{Sample Size}}{\text{Size of Population from which Sample Taken}} \tag{5.2}$$

So, suppose that there were x males and y females in a population, and that half the females sampled only one male and the other half of the females sampled two males. The average male can expect to be in $y/(2x)$ samples taken by females who sample only one male as by equation (5.2):

$$\text{Frequency of Being in Sample of Size 1} = \frac{(y/2)\times(1)}{x}$$

whilst the average male can expect to be in $y/x = 2\cdot(y/(2x))$ samples taken by females who sample two males as by equation (5.2):

$$\text{Frequency of Being in Sample of Size 1} = \frac{(y/2)\times(2)}{x}$$

In the rest of this chapter, it will be assumed that the expected number of samples that a male appears in during the lifetime of a given signal is given by $\Lambda(D,n)D'(n)$. In general:

$$(n+m)\Lambda(n) = n\Lambda(n+m).$$

5.2 Additive Model, Error Free Signalling

5.2.1 C and K Independent of A

Any level of female discrimination leads to a splitting equilibrium in the model of male advertising in section 2.2. As there is no error in signalling and no effects of male advertising upon the population structure, the benefits of choosing from n is independent of the particular splitting equilibrium. Thus, the splitting equilibrium strategies may be calculated independently. If $D(1) \neq 1$ then Proposition 2.1 shows that there exists a signalling equilibrium, $\{D, A\}$ where A is the unique solution to the differential equation:

$$\frac{dA}{dq} = \frac{V(q) \int_1^{n(q_{\max})} (n-1) f(q) F^{n-2}(q) \Lambda(n) D'(n) \cdot dn}{C_1(A(q), q)}$$

satisfying $A(q_{\min}) = a_{\min}$. If $D'(n) = 0$ for almost all $n \in [1, 2]$ then Proposition 2.1 shows that this ESS is the unique signalling ESS, as the integral is then Lipschitz in q. The integral is weighted by the factor $nD'(n)$ although $D'(n)\delta n$ females sample between n and $n + \delta n$ males. The reason is slightly subtle (see section 5.1.3).

Obviously, there also exists a non-signalling ESS where all the males signal at $a_{\min}$ and none of the females are discriminating. (Note that as $N \in N'(5)$ this is technically not correct. However, the definition of $N'(5)$ is made under the assumption that females are discriminating in some sense, so this case should be treated separately.)

5.2.2 C and/or K Continuously Dependent upon A

If C and/or K is a function of A, then the 'trick' used above to calculate male and female splitting equilibrium strategies separately can no longer be used. This is because one or both of the male or female strategies is dependent upon the other. A method of dealing with this problem is outlined in section 3.2 and it is used here explicitly.

As $K_{22} > 0$ and $E(R, x)$ is bounded above for all A, there exists $n_{\max}$ so that it cannot be an optimal strategy for a female of any quality to discriminate amongst more than $n_{\max}$ males. Female strategies may thus be represented by increasing functions, D, which satisfy $D(1) \geq 0$ and $D(n_{\max}) = 1$. Set:

$$\mathcal{D} = \{D(n);\ D : [1, n_{\max}] \to [0, 1] \text{ increasing in } n\ \}$$

$\mathcal{D}$ thus contains all possible ESS strategies for females. Clearly $\mathcal{D}$ is a compact convex subspace of $\mathcal{L}_1([1, n_{\max}])$ by Lemma 4 of Grafen(1990a).

By equation (2.7) there exists $a_{\max}$ for which $C(A, a_{\max}, q) > R(q_{\max})$ for all A and q. Set $\mathcal{S}$ to be the set of all increasing functions from $\mathcal{Q} \to [a_{\min}, a_{\max}]$. Clearly $\mathcal{S}$ is compact and convex, and by Tyconoff's Theorem so is $\mathcal{D} \times \mathcal{S}$:

Define:

$$M_{\mathcal{D}}\{D, A\} = D(A)$$

and:

$$M_{\mathcal{S}}\{D, A\} = \frac{V(q) \int_1^{\infty} (n-1) f(q) F^{n-2}(q) \Lambda(n) \frac{\partial D(A,n)}{\partial n} \cdot dn}{C_2(A, A(q), q)}$$

Clearly $M_{\mathcal{D}}$ sends $\mathcal{D} \times \mathcal{S}$ continuously into $\mathcal{D}$. Moreover the image of $M_{\mathcal{D}}$ consists entirely of absolutely continuous functions, which implies that $M_{\mathcal{S}}$ is well defined. It is also clear that $M_{\mathcal{S}}$ sends $\mathcal{D} \times \mathcal{S}$ into $\mathcal{S}$ continuously.

Schauder's Theorem, then implies that there exists a fixed point of the map:

$$(M_{\mathcal{D}} \times M_{\mathcal{S}}) \circ \Delta : \mathcal{D} \times \mathcal{S} \to \mathcal{D} \times \mathcal{S}$$

This fixed point is then a combined signalling/receiving ESS, provided that $D(1) \neq 1$. It is trivial to show that if $R_2(A, q) > 0$ for all $A \in \mathcal{S}$ and $K_2(A, 1, q) = 0$, then $D(1) = 1$ cannot be an ESS, so there exists circumstance in which a signalling equilibrium exists.

As in the previous example, a non-signalling equilibrium can also exist.

5.2.3 Perceived Quality Dependence

If payoffs are perceived-quality-dependent then there exists at least one discriminating/signalling ESS, derivable as above, *mutatis mutandis*. Note that if females play $D(1) = 1$, and $V(A, a) \in \mathcal{N}(1 - 9)$, the best male response is the unique solution to:

$$\frac{dA}{dq} = \frac{V'(q)}{C_1(A(q), q)}$$

with $A(q_{\min}) = a_{\min}$. This is a splitting ESS, as it is assumed that $V' > 0$ almost everywhere.

Perceived quality payoffs to males thus provide the theoretical possibility that exaggerated male traits may still be inter-sexually selected in situations where females choose mates by their territories, or randomly select mates. Although the chance of a male obtaining a mate may be independent of his actual quality, it may be the case that females have a differential willingness to invest in a male's offspring, dependent upon his perceived quality (Burley 1988). If investment in offspring is costly to females, then it may be optimal for females to reduce investment in a poor quality brood.

If $N \in \mathcal{N}(5)$ is assumed not to hold when $D(1) = 1$, then a non-signalling ESS is also possible.

5.3 Multiplicative Model, Error Free Signalling

In the first instance, assume that all females sample n males. The payoff to a male of quality q advertising at a in a population where males advertise at $A(q)$ is, assuming that $A'(q) > 0$ a.e., proportional to:

$$S(A, a, q) \left(\frac{\int_{q_{\min}}^{A^{-1}(a)} S(A, A(r), r) f(r) \cdot dr}{\int_{q_{\min}}^{q_{\max}} S(A, A(r), r) f(r) \cdot dr} \right)^{n-1} V^p(A, q) V^q(A, q),$$

where the ratio of integrals is the post selection cumulative distribution function of qualities of adult males in a population advertising with strategy $A(q)$, if $f(q)$ is probability density of qualities before selection.

For $n > 1$ the first order condition for an ESS is:

$$\frac{dA^*}{dq} = \frac{S(A^*, A^*(q), q)}{S_2(A^*, A^*(q), q)} \left(\frac{(1-n)S(A^*, A^*(q), q)f(q)}{\int_{q_{\min}}^{q} S(A^*, A^*(r), r)f(r) \cdot dr} - \frac{V_2^p(A^*, q)}{V^p(A^*, q)} \right)$$

This equation creates an interesting problem; the right hand side of the equation goes to infinity as $q \to q_{\min}$. Under certain conditions this may not be a problem, as a solution to the differential equation may still exist (consider the equation $\dot{x} = t^{-\frac{1}{2}}$ with initial condition $x(0) = 0$), but this will not be the case in general for the above equation as:

$$\int_{q_{\min}+2\epsilon}^{q} \frac{S(A^*, A^*(p), p)f(p)}{\int_{q_{\min}+\epsilon}^{p} S(A^*, A^*(r), r)f(r) \cdot dr} \cdot dp = \ln \left(\frac{\int_{q_{\min}+\epsilon}^{q} S(A^*, A^*(r), r)f(r) \cdot dr}{\int_{q_{\min}+\epsilon}^{q_{\min}+2\epsilon} S(A^*, A^*(r), r)f(r) \cdot dr} \right)$$

and the right hand side of this equation does not exist as $\epsilon \to 0$.

An individual advertising at the lowest level in the population cannot expect to win any contests in his lifetime. Thus, if the only way to obtain mates is by winning advertising contests, the individual's expected lifetime reproductive success will be zero. Further, there would be nothing lost in decreasing the male's life-span so long as it gave him even the minutest chances of obtaining a mate. Mathematically this appears in the equation as an infinite gradient for A^* at $q_{\min}$. This is the Desperado Effect of Grafen (1987; see also Enquist & Leimar 1990) which, potentially, must be addressed in any model in which fitness is multiplicative.

The Desperado Effect relies on the fitness of a signaller which is perceived as being of the lowest quality being at its absolute minimum. In a multiplicative model, this is when fitness is zero; in an additive model, the equivalent circumstance is when payoff is $-\infty$ (i.e. $\ln 0$). Therefore, the worst problems of the Desperado Effect are avoided in the case of sexual selection if for instance:

- A signaller can gain fitness outside of the signalling game, for example by forced copulations (e.g. Cramp & Simmons 1977; Burns et al. 1980);
- Receivers make mistakes in perceiving the level of signal (see section 5.4);
- Receivers are not always choosey. For example, in the case of monogamous species, it may be better for a female to be the sole mate of the worst possible male, than being a secondary mate of a high quality male (see Slagsvold & Lifjeld 1994). In a species which utilizes sequential mate search, there may be a time after which it is best to accept any male (Grafen 1990a; Johnstone 1997);
- Signaller quality increases with age (Trivers 1972; Halliday 1978; Weatherhead, 1984; see also Shutler & Weatherhead 1992); and
- The signaller may improve its quality for the next breeding season by not breeding (Partridge & Harvey 1988).

In summary, the extreme Desperado Effect seen above is avoided if an individual has either a future expectation of reproductive success, or can obtain reproductive success without signalling. Individuals should only escalate contests desperately if all or almost all of their expected lifetime reproductive success hinges on the outcome.

For the purpose of exposition, conditions on K will be assumed so that there exists a proportion of females in the population for which it is too costly to discriminate. This implies that even the lowest quality males have a chance of mating, thus introducing a cost to decreasing survival by advertising above $a_{\min}$ for individuals of the lowest quality. Grafen's model (1990a) makes assumptions that lead to a similar situation (see section 6.2).

The difference between the multiplicative model of section 2.3 and the additive model of section 2.2 is, in essence, that the male population structure is dependent upon the male population advertising strategy, $A(q)$. Thus, the benefit to females of discrimination is dependent upon $A(q)$, as I is dependent upon A through x.

For ease of analysis, it is assumed that K is independent of A. As, given the form of the female strategy, any male signalling ESS must be strictly increasing, it will be useful to calculate the optimal female response to a male strategy that is not strictly increasing as if it were separating (see section 2.3). This makes $D(A, n)$ continuous in A, without missing any plausible ESSs, except the non-discriminating ESS ($D(1) = 1$). Also note that, as $\mathcal{S}$ is compact and $I_2(A, 1)$ is continuous in A, there exists A^{sup} for which $I_2(A^{\text{sup}}, 1) \leq I_2(A, 1)$ on $\mathcal{S}$. Assume that $D(A^{\text{sup}}, 1) = d > 0$. Similar arguments show that there exists an n_{max} for which no $n > n_{\text{max}}$ can be a solution to:

$$I_2(A, n) = K_1(n, q)$$

for $A \in \mathcal{S}$. For the purpose of demonstration, assume that S satisfies the conditions of Case 1 of Proposition 2.3. The payoff to a male of quality q playing a in a population playing A is given by:

$$P(A, a, q) = V^p(A^{-1}(a))V^q(q)\left(\int_1^{n_{\max}} F^{n-1}(A, S, A^{-1}(a))\Lambda(n)D'_{\circ}(n)\cdot dn + \Lambda(1)D(1)\right) S(A, a, q)$$

where:

$$F(A, S, q) = \frac{\int_{q_{\min}}^{q} S(A, A(r), r)f(r)\cdot dr}{\int_{q_{\min}}^{q_{\max}} S(A, A(r), r)f(r)\cdot dr}$$

Consider the subspace $\mathcal{D} \times \mathcal{S} \subset \mathcal{L}_1([1, n_{\text{max}}]) \times \mathcal{L}_1(\mathcal{Q})$, where $\mathcal{S}$ is as in Proposition 2.3 and:

$$\mathcal{D} = \{D(n);\ D \text{ increasing}, d \leq D(n) \leq 1\}$$

$\mathcal{D} \times \mathcal{S}$ is bounded and is compact by Tychonoff's Theorem (Munkres 1975, p232). Furthermore, $\mathcal{D} \times \mathcal{S}$ is homeomorphic to a convex space.

As in section 5.2, the idea is to find a fixed point of the map $M_{\mathcal{D}} \times M_{\mathcal{S}} \circ \Delta$ where:

$$M_{\mathcal{D}}\{D_{\circ}, A\} = D(A)$$

and:

$$M_{\mathcal{S}}\{D_{\circ}, A\} = M(\{D_{\circ}, A\})$$

where $D(A)$ is the females' best response to a population of males advertising at A, as defined in section 5.1 and $M(\{D_{\circ}, A\})$ is the solution to the differential equation derived from the payoff function:

$$\frac{dM(A)}{dq} = \frac{\int_1^{n_{\max}} \left((1-n)F^{n-2}(A,S,q)F_3(A,S,q) - \frac{V_2^p(A,q)}{V^p(A,q)}\right)\Lambda(n)D_o'(n)\cdot dn - \Lambda(1)D_o(1)\frac{V_2^p(A,q)}{V^p(A,q)}}{\Lambda(1)D_o(1) + \int_1^{n_{\max}} F^{n-1}(A,S,q)\Lambda(n)D_o'(n)\cdot dn} \times \frac{S(A,A(q),q)}{S_2(A,A(q),q)}$$

with initial condition $M(A)(q_{\min}) = a_{\min}$. Note that $M(A)$ is strictly increasing for all A if $V_2^p(A,q) > 0$ for all q, and thus into $\mathcal{S}$. This is the best response to A if A is continuous and strictly increasing.

Clearly, $M_{\mathcal{D}} \times M_{\mathcal{S}} \circ \Delta$ is continuous as both D and M are. Thus the conditions of Schauder's Theorem are satisfied, implying that there exists at least one fixed point of $M_{\mathcal{D}} \times M_{\mathcal{S}} \circ \Delta$, which in turn implies that there exists at least one discriminating/signalling female/male ESS if $V_2^p(A,q) > 0$ (a sufficient condition only). If this condition is not satisfied by V^p, then a specific calculation is necessary. The existence of a non- signalling/non-advertising ESS is dependent on the form of V^p as noted in section 5.2.3.

5.4 Additive Model, Error-Prone Signalling

Assume females use a pool-comparison sampling technique, and that they have a normally distributed error in perception, with standard deviation σ_f. Males are assumed to have normally distributed error in realization of their signal with standard deviation σ_m. Fitness is assumed to be partitioned additively.

5.4.1 Basic Facts About Male Strategy

The proportion, x, of males in a population with signalling strategy A that are perceived to be advertising at a level p or less is given by:

$$x(A,p) = \frac{1}{\sqrt{2\pi(\sigma_m^2 + \sigma_f^2)}} \int_{-\infty}^{p} \int_{Q} \exp\left(\frac{-(A(q)-b)^2}{2(\sigma_m^2+\sigma_f^2)}\right) f(q)\cdot dq\,db$$

assuming that error in perception and realization are independent. Lemma B.1 implies that if $A(q)$ is increasing, then females should select the male that is perceived as signalling at the highest level (unless $A(q)$ is constant, in which case arbitrary choice gives an equal payoff). Using the notation for additive models this gives the male payoff:

$$P(A,a,q) = \frac{V^q(q)\Lambda(n)}{\sqrt{2\pi(\sigma_m^2+\sigma_f^2)}} \int_{-\infty}^{\infty} V^p(A,p)\exp\left(\frac{-(a-p)^2}{2(\sigma_m^2+\sigma_f^2)}\right) x^{n-1}(A,p)\cdot dp - \bar{C}(A,a,q)$$

where $\Lambda(n)$ is the expected number of contests that an individual male will be involved in over the lifetime of the signal, and:

$$\bar{C}(A,a,q) = \frac{1}{\sqrt{2\pi}\sigma_m} \int_{-\infty}^{\infty} C(A,b,q)\exp\left(\frac{-(a-b)^2}{2\sigma_m^2}\right)\cdot db$$

Proposition 2.4 implies that for any given female strategy (i.e. for any given value of n) there exists at least one male ESS, which may be the non-signalling $A(q) = a_{\min}$ or $A(q) = a_{\max}$ for all q, provided that either $a_{\max} < \infty$ or there exists an $a < \infty$ so that for all A:

$$V^q(A, q_{\max})V^p(A, \infty)\Lambda(n) < \tilde{C}(A, a, q_{\max})$$

(This restriction is necessary because it is not possible to treat Gaussian error sensibly for a male attempting to advertise at $a = \infty$.)

5.4.2 Female Strategy

The calculation of the optimal female strategy in the error-prone signalling case differs in only one significant aspect from the error-free case. At a splitting equilibrium in the error-prone situation, females cannot infer a male's quality from his perceived level of signal. However, Lemma B.1 shows that if A is increasing in male quality, then a female's expected reproductive success is increasing in the perceived level of advertising. R and x in Proposition 5.1 are then assumed to be functions of perceived level of signal p instead of male quality q. This change does not affect the qualitative nature of the result.

5.4.3 Interaction of Male and Female Strategies

The modular approach outlined in section 3.2 can be applied to the model as follows. Set $\mathcal{S} = \{A(q); A(q) \text{ increasing}, a_{\min} \leq A(q) \leq a_{\max}\}$, where for convenience we assume that $a_{\max} < \infty$. As $\mathcal{S}$ is compact, $K_{22} > 0$, and I is continuous in A we know that there is an upper bound $n_{\max}$ for which no $n > n_{\max}$ can be a solution to $I_2(A, n) = K_2(A, n, q)$ (see section 5.3 for more explicit reasoning on this point). Thus, the set of possible optimal female strategies for all $A \in \mathcal{S}$ is contained in:

$$\mathcal{D} = \{D(n);\ D : [1, n_{\max}] \to [0, 1] \text{ increasing in } n\ \}$$

Clearly, $\mathcal{D}$ and $\mathcal{S}$ are compact and convex and thus so is $\mathcal{D} \times \mathcal{S}$.

As in section 5.2, the idea is to find a fixed point of the map $\mathcal{M}_{\mathcal{D}} \times \mathcal{M}_{\mathcal{S}} \circ \Delta$ where:

$$M_{\mathcal{D}}\{D_o, A\} = D(A)$$

and:

$$M_{\mathcal{S}}\{D_o, A\} = A_R(D)$$

where $D(A)$ is the females' best response to a population of males advertising at A, as defined in section 5.1 and $A_R(D)$ is the choice function in [4] of the proof of Proposition 2.4, after identifying:

$$\begin{aligned} V^p(A, a)N(A, a) \quad = \quad & \int_1^{n_{\max}} \frac{\Lambda(n)}{\sqrt{2\pi(\sigma_m^2 + \sigma_f^2)}} \int_{-\infty}^{\infty} V^p(A, p) \exp\left(\frac{-(a-p)^2}{2(\sigma_m^2 + \sigma_f^2)}\right) x^{n-1}(A, p) \frac{\partial D(A, n)}{\partial n} \cdot dp dn \\ & + D(1) \frac{\Lambda(1)}{\sqrt{2\pi(\sigma_m^2 + \sigma_f^2)}} \int_{-\infty}^{\infty} V^p(A, p) \exp\left(\frac{-(a-p)^2}{2(\sigma_m^2 + \sigma_f^2)}\right) \cdot dp \end{aligned}$$

$M_{\mathcal{D}} \times M_{\mathcal{S}} \circ \Delta$ is clearly continuous in both D and A and Schauder's Theorem implies that an ESS exists.

It should be noted that $D(1) = 1$ and $A(q) = a_{\min}$ is always a fixed point of $M_{\mathcal{D}} \times M_{\mathcal{S}} \circ \Delta$. However, examples can be constructed in which this is not the only fixed point.

5.4.4 Error in Development and the Non-Existence of Non-Signalling Equilibria

Provided receiver costs are low enough, the models of error-free signalling in sections 5.2 and 5.3 can be guaranteed to have non-signalling equilibria. As noted above, this is not immediately obvious in the error-prone signal case, apart from constructed examples for which one does not need a general theory.

Proposition 4.2 of section 4.1 does not alleviate this problem when receiver strategies are allowed to evolve in response to the population signalling strategy. This is because the increase in the receivers' fitnesses due to discrimination between signals is dependent upon how well they can separate individuals of different quality. For error in perception which has variance independent of the slope of the signalling strategy, this ability to separate different qualities decreases to zero as the population strategy decreases to $A(q) = a_{\min}$ for all $q \in Q$. Thus, it is possible that the signallers' best responses for each given level of discrimination by the receivers may not separate signallers of different qualities enough to support the given level of discrimination in the receiver population. In this case, the only dual equilibrium strategy would be no discrimination and no signalling.

There does not appear to be a general result showing when there are and are not signalling/receiving equilibria in models in which there is error in signalling and this error is solely due to receiver's perceptions. However, the situation in which signals suffer from error in realization, is somewhat different. In this case, there are clearly definable conditions under which there is no non-signalling/non-discriminating equilibrium. These conditions are best discussed in the sexual selection/multiplicative partition of fitness case.

In this situation, females may be discriminating even when the male population's signalling strategy is $A(q) = a_{\min}$. Although prior to the effects of the level of signal borne on the male population structure, the expected quality of males is independent of the level of signal developed, Lemma B.1 tells us that expected quality of signaller is strictly increasing in the perceived level of signal, provided S satisfies:

$$\frac{\partial}{\partial q}\left(\frac{S_2(a_{\min}, a, q)}{S(a_{\min}, a, q)}\right) > 0 \quad .$$

Recall that the above equation states that a signaller of low quality suffers a greater relative decrease in survival when bearing a non-optimal signal than a high quality signaller. (To apply Lemma B.1 the differential costs to survival must be incurred, at least partially, before the signals are received. That is, the order of events must be: develop signal, incur cost of signal, receive benefit of signal. Clearly, no correlation between signal and quality of signaller would be observed if the cost of the signal was incurred after the benefit was obtained.) So, provided that the costs of discrimination to females is small, they will benefit from mating with males who bear larger signals.

The epistatic handicap model of chapter 9 is identical with the strategic handicap model outlined here when $A(q)$ is constant. Therefore, Example 1 of section 9.7 provides a calculation of the conditions necessary for the females' optimal strategy to be discriminating when the male population develops signals with mean $A(q) = a_{\min}$. As in Example 1 of section 9.7, this calculation may be extended trivially to show conditions under which the males best response to the females best response to a male population which develops signals with mean $A(q) = a_{\min}$ is not $A(q) = a_{\min}$.

5.5 Comparison with Sequential Choice

This section shows that the mechanism of female choice may have qualitative effects upon male advertising strategies, by comparing the male ESS for females using a sequential method of discrimination, with the male ESS for a population of females who use the pool-comparison method of discrimination. Unfortunately, the second model of female choice does not lead to an N which satisfies the conditions assumed in the models of chapter 2 in its most simple formulation.

> **Outline:** A females visit males and decide whether to mate or whether to find another male. If the female decides to find another male, she cannot go back to any of the previous males sampled. The distribution of male reproductive success, by quality, is determined, as is the distribution of number of males sampled per female.

This model is similar to, but not the same as, the model of female choice in Grafen (1990a), but is identical with the 'one-step decision process' of Janetos (1980; see also Janetos & Cole 1981; Houston & McNamara 1984; Real 1990, 1991). As well as sexual selection, this model of receiver behaviour is perhaps particularly applicable to predator-prey models—where a predator must decide whether to chase a given prey item or ignore it and search for another.

It is obvious, in the case of this model of female choice, that the optimal female strategy to a separating male advertising strategy may be represented as a series of threshold perceived advertising levels. Let $k(n)$ denote difference in cost to female between sampling n and $n-1$ males (i.e. $K(n) - K(n-1)$ in the pool-comparison model). It is assumed that $k(n) > 0$ for all $n \geq 2$, and that $k(n)/k(n+1) \leq \kappa < 1$. Under these conditions, there exists an $n_{\max}$ at which a female should settle for the male with whom she is with. An upper bound on this is easily seen to be any n which satisfies:

$$\kappa(R(q_{\max}) - R(q_{\min}))^{\frac{1}{n}} \leq 1$$

Given this upper bound, we may calculate the threshold values using a simple dynamic programming technique.

While the calculation of threshold levels is reasonably easy to represent, the interaction with male strategies becomes rather complex. It is reasonably simple in the case where the cost of leaving the second male visited is always prohibitive, i.e. when:

$$\int_{q_{\min}}^{q_{\max}} R(q)f(q) \cdot dq - R(q_{\min}) < k(3),$$

which shall be assumed for the purpose of demonstration; the design of introducing this second model of female choice is to show how female decision rules may have qualitative effects on male strategy, not to provide an exhaustive analysis of a second mechanism of female choice.

In this case the female strategy may be represented by a single valued function, which sends the male advertising strategy to the threshold value at which she discards the first male she finds in favour of finding another. If the male advertising strategy, A, is increasing and separating, then the ESS threshold value for the female strategy is given by:

$$A \circ R^{-1}\left(\int_{q_{\min}}^{q_{\max}} R(q)f(q) \cdot dq - k(2)\right) \overset{\text{def}}{=} a_t$$

where $R^{-1}(v) = q_{\min}$, if $v \leq R(q_{\min})$.

If signals are error-prone, then A will not, in general, be separating. In this case a_t is defined as the signal level at which the expectation value of R is the same as that of individuals of quality:

$$R^{-1}\left(\int_{q_{\min}}^{q_{\max}} R(q)f(q) \cdot dq - k(2)\right)$$

5.5.1 Male ESS, Additive Model with Actual Quality Dependent Payoff

The best male response to a population whose males play a strictly increasing strategy, A, and females use the sequential method of assessing males, is the strategy :

$$A_R(q) = \begin{cases} 0 & \text{if } q < q_c \\ a_t & \text{if } q > q_c \\ 0 \text{ or } a_t & \text{if } q = q_c \end{cases}, \tag{5.3}$$

where q_c is defined implicitly by:

$$\frac{1}{1 + F(A^{-1}(a_t))} - \frac{C(a_t, q_c)}{V(q_c)} = 0$$

The first term in the above expression is the proportion of females that, having visited a male advertising below a_t, would choose to search for another male. If no such q_c exists, then the best response is for all males to signal at a_t (which may be represented by choosing $q_c < q_{\min}$). This strategy is clearly not separating, and thus no separating male advertising strategy can be part of a joint ESS. It is easy to see that any strategy that is not a single or two-step function, like equation (5.3), cannot be a male ESS.

Suppose $A(q)$ is a two-step function (the notation of equation (5.3) is used, but no relationship between a_t and q_c with the optimal female strategy for a separating equilibrium is assumed). Then the female strategy 'accept the first male only if he advertises at a_t or above', is an ESS provided:

$$\int_{q_c}^{q_{\max}} R(q)f(q) \cdot dq < k(2)$$

This female strategy and $A(q)$ is a joint ESS if and only if q_c satisfies:

$$\frac{1}{1+F(q_c)} - \frac{C(a_t, q_c)}{V(q_c)} = 0$$

As further analysis of this case would necessitate justifications of out of equilibrium behaviour of females, it will not be taken any further. The point of significance is that the above male advertising ESS is qualitatively different from the ESS obtained for the male strategy in Proposition 2.1. If, contrary to the assumption in the previous section, the cost of leaving the second male is not always prohibitive, but instead the cost of leaving the nth male is, then the male strategy would be a step function of *at most* n steps.

5.5.2 Male ESS, Additive Model with Perceived Quality Dependent Payoff

Assuming that $V''(q) > 0$, there exists a male ESS that is separating in response to the female threshold strategy. Define:

$$q_t = R^{-1}\left(\int_{q_{\min}}^{q_{\max}} R(q)f(q) \cdot dq - k(2)\right)$$

Scaling N so that $N(q) = 1$ for $q > q_t$, the following function is the unique male ESS:

$$A^*(q) = \begin{cases} \frac{dA^*}{dq} = \frac{V'(q)F(q_t)}{(1+F(q_t))C_1(A^*(q),q)} & A^*(q_{\min}) = a_{\min} \quad q \in [q_{\min}, q_t) \\ \frac{dA^*}{dq} = \frac{V'(q)}{C_1(A^*(q),q)} & A^*(q_t) = a_t \quad q \in (q_t, q_{\max}] \end{cases}$$

where $A^*(q_t)$ is either a_t or $a_{\lim} = \lim_{q \uparrow q_t} A^*(q)$, and a_t is defined implicitly by:

$$C(a_t, q_t) = \frac{V(q_t)}{1+F(q_t)} - C(a_{\lim}, q_t)$$

If, instead of the assumption that rejecting the second male is prohibitively costly, the female costs are such that the nth male is the one for which it is always prohibitively costly to reject, the male ESS strategy would be a step-like function of *precisely* n steps.

5.5.3 Actual Quality Dependent, Females Have Costs Distributed

This section relates to a situation similar to the above, but it is assumed that $k(2)$ is not the same for all females; that is, females vary in quality. Denote by $H(q)$ the cumulative distribution of females who will accept the first male that they visit if he signals at or above q (assuming a splitting male equilibrium for all male qualities for which $H(q) \neq 1$). Clearly, $H(q) = 1$ for all q such that:

$$R(q) > \int_{q_{\min}}^{q_{\max}} R(q)f(q) \cdot dq \overset{\text{def}}{=} R(\bar{q}).$$

as a female which rejects the first male that she samples can only expect to obtain a male of mean reproductive value. As H is a distribution function it is absolutely continuous.

The payoff to a male of quality q advertising at a in a population playing a splitting equilibrium A is:

$$\frac{H(A^{-1}(a)) + \int_Q F(q)H'(q)\cdot dq}{1 + \int_{q_{\min}}^{q_1} F(q)H'(q)\cdot dq} V(q) - C(a,q)$$

where the integral represents the proportion of females that choose to search for a second male. This has been integrated by parts from $\int(1-H)f \cdot dq$ to give a simpler form. This is made under the assumption that the signal's lifetime is precisely one contest, and that the male signals without knowledge whether he is the first or second male that the female has visited.

The first order condition for an ESS is given by:

$$\frac{H'(q)}{1 + \int_Q F(q)H'(q)\cdot dq} V(q) - C_1(A(q),q)\frac{dA}{dq} = 0$$

By arguments similar to those adduced in Proposition 2.1, the male advertising ESS is the solution to the above first order condition with initial condition $A(q_{\min}) = a_{\min}$. It should be noted that this solution is constant on $[q_1, q_{\max}]$, where $q_1 \overset{\text{def}}{=} \min\{q; H(q) = 1\}$.

If the cost of searching is basically the same for all females (i.e. $H(q)$ goes from close to 0 to close to 1 over a small range of qualities), then the solution to the above equation will closely approximate a step function. As the variance in female costs increases, the solution will become less and less like a step function.

5.5.4 Example Comparison Between Pool-Comparison and Sequential Choice

The effects of the different female discrimination strategies on the male ESS signalling strategy are perhaps best exhibited by a simple example. An additive partition of male fitness will be assumed. It will also be assumed throughout the following, that V is constant, $C(a,q) = a/q$ (and is implicitly independent of A), $q_{\min} > 0$, the male population structure is unaffected by the population advertising function, and:

$$f(q) = \frac{1}{q_{\max} - q_{\min}}$$

As in section 5.2.1, the male and female ESS strategies are decoupled under these conditions. It is also assumed that the male advertisement lasts the entire breeding season, females mate once, and the ratio of females to males is Λ.

Pool-Comparison: To facilitate comparison with the sequential choice model, assume that the costs of female discrimination are such that females sample at most two males. Denote by d_p the probability that they sample two males. By Proposition 2.1, the ESS male signalling strategy, A_p, is given by the differential equation:

$$\frac{dA_p}{dq} = \frac{2\Lambda V q d_p}{q_{\max} - q_{\min}} \tag{5.4}$$

with initial condition $A_p(q_{\min}) = a_{\min}$. This may be integrated to give:

$$A_p(q) = a_{\min} + \frac{\Lambda V(q^2 - q_{\min}^2)d_p}{(q_{\max} - q_{\min})}$$

Sequential Choice: Assume that:

$$H(q) \stackrel{\text{def}}{=} \begin{cases} 0 & q \in [q_{\min}, q_\alpha) \\ \frac{q - q_\alpha}{q_\beta - q_\alpha} & q \in [q_\alpha, q_\beta] \\ 1 & q \in (q_\beta, q_{\max}] \end{cases}$$

The case $q_\alpha < q_{\min}$ can be interpreted as the situation in which some females never sample more than one male. It is always assumed that $q_\beta \in [q_{\min}, q_{\max}]$. Define:

$$d_s \stackrel{\text{def}}{=} \int_Q F(q) H'(q) \cdot dq$$

d_s is the proportion of females that sample two males. A simple calculation shows that:

$$d_s = \begin{cases} \frac{(q_\beta - q_{\min})^2}{2(q_\beta - q_\alpha)(q_{\max} - q_{\min})} & q_\alpha \leq q_{\min} \\ \frac{q_\beta + q_\alpha - 2q_{\min}}{2(q_{\max} - q_{\min})} & q_\alpha \geq q_{\min} \end{cases}$$

From section 5.5.3, the ESS male signalling strategy, A_s, is given by the differential equation:

$$\frac{dA_s}{dq} = \begin{cases} 0 & q \in [q_{\min}, q_\alpha) \\ \frac{\Lambda V q}{(q_\beta - q_\alpha)} & q \in [q_\alpha, q_\beta] \\ 0 & q \in (q_\beta, q_{\max}] \end{cases}$$

with initial condition $A_s(q_{\min}) = a_{\min}$. This differential equation may be integrated to give:

$$A_s(q) = \begin{cases} a_{\min} & q \in [q_{\min}, q_\alpha) \\ a_{\min} + \frac{\Lambda V(q^2 - q_\alpha^2)}{2(q_\beta - q_\alpha)} & q \in [q_\alpha, q_\beta] \\ a_{\min} + \frac{\Lambda V(q_\beta + q_\alpha)}{2} & q \in (q_\beta, q_{\max}] \end{cases}$$

if $q_\alpha \geq q_{\min}$. If $q_\alpha < q_{\min}$ then:

$$A_s(q) = \begin{cases} a_{\min} + \frac{\Lambda V(q^2 - q_{\min}^2)}{2(q_\beta - q_\alpha)} & q \in [q_{\min}, q_\beta] \\ a_{\min} + \frac{\Lambda V(q_\beta^2 - q_{\min}^2)}{2(q_\beta - q_\alpha)} & q \in (q_\beta, q_{\max}] \end{cases}$$

The most obvious difference between the two sampling strategies is their effect on the shape of the male signalling equilibrium. If females differ little in their costs of sampling then one-step sequential choice leads to an S-shaped male advertising ESS; at its most extreme this strategy looks very similar to a dimorphic (see section 7.2) or 'all or nothing' (Johnstone 1994) signalling ESS. On the other hand, regardless of the distribution of costs of discrimination, pool-comparison sexual selection leads to a parabolic relationship between male quality and level of signal at the ESS.

6 Comments on Previous Biological Models

6.1 Best of n Games

6.1.1 The Opponent Independent Costs Game

The games solved in section 2 are a generalized form of the Opponent Independent Costs Game (OICG) of Parker (1979, 1983; Rose 1978; Haigh & Rose

1980). The continuous strategy set formulation of the original game is identical, except in the one aspect outlined below, to the additive game (equation (2.1)) with N defined by the pool-comparison strategy (see section 4.2 and chapter 5) from a pool of two individuals.

Parker (1979) hypothesized, and Rose (1978) proved, that there is no ESS to the OICG as originally formulated, though a Nash equilibrium does exist (Rose 1978, Parker 1983a for further references). Haigh & Rose (1980) showed that an ESS was obtained if winners did not pay the full cost of escalating (see below). However, this solution does not seem to be appropriate for some of the biological contests that motivated the OICG, i.e. the development of armaments and sexually selected exaggerated traits whose cost is independent of the opponents level of escalation (e.g. peacocks' tails).

Parker (1983a) has provided a more appropriate solution. He found that if the development of the trait could not be perfectly controlled and, thus, there was a certain amount of unavoidable variance in the expression of the trait, then ESSs could exist. However, these ESSs, whilst being appropriate for the analysis of the evolution of weapons, are not relevant to the evolution of traits which benefit the bearer by increasing their reproductive success because more (or more fecund) members of the opposite sex wish to mate with them. This is because these ESSs are pure and all individuals are identical in their ability to bear the trait, conditions under which strategic discrimination by receivers cannot exist if it is in some sense costly, as there is absolutely no benefit to be gained by such discrimination (chapter 9). The continuous epistatic handicap model of chapter 9 rectifies this problem in a model that is identical with Parker's (1983a) multiplicative OICG by assuming that there is variance in individual quality and that the survival, S, of individuals is quality dependent, and satisfies equation (2.12).

The games provided here solve the OICG ESS problem in another way. The difference between the original OICG and the additive game defined by equation (2.1) is that Parker(1979) and Rose (1978) assumed that individuals all valued the resource identically, and that all individuals paid the same costs to escalate to a given level. In the games presented here, individuals vary in their valuation of resources and cost of escalation. This variation turns the Nash equilibrium of the OICG into an ESS.

6.1.2 The War of Attrition with Continuous Random Rewards

In the War of Attrition (WOA), individuals are involved in a conflict over resources which is resolved by a process of continuous escalation. Each individual may choose when to stop escalating, the winner of the resouce being the sole indivdiual not to quit. If there is a tie, when the last players all quit simultaneously, the resource is divided equally amongst these individuals, or equivalently, the winner is chosen randomly from the tying individuals. There is a cost to escalating, and individuals pay an amount proportional to the level to which they escalate. The winner pays an amount proportional to the level to which the last individual to quit escalates.

As can be seen from the above description, the only difference between the WOA and the Opponent Independent Cost Game (OICG), is the cost paid by the winner. In the OICG the winner pays as much as if it had escalated to the highest level to which it was willing to escalate, whilst in the WOA the winner pays the cost appropriate to the level escalated by the last individual to quit.

Here it is shown that Proposition 2.1 gives, as a corollary, models similar to Haigh and Rose's (1980) which encompass the War of Attrition with continuous random rewards (result given without proof in Bishop et al. 1978; see also Riley 1980). The results presented differ from previous WOA models, in that the competition is assumed to be between $n+1$ individuals randomly selected from a population whose costs of escalation and valuation of the contested resources are continuously distributed.

Haigh & Rose (1980) generalized the WOA and OICG by adding an overshoot function to the cost incurred by the winner. There is no single obvious way of generalizing the overshoot function to the case in which individuals vary in quality continuously. Two possible generalizations are given below.

Generalization 1: Consider the best of n game for which the payoffs are given by:

$$\text{Payoff} = \begin{cases} -\hat{C}(a_q, q) & \text{lose} \\ U(a_r)V(q) - \lambda(q)\hat{C}(a_r, q) - (1-\lambda(q))\hat{C}(a_q, q) & \text{win} \\ U(a_r)V(q)/(m+1) - \hat{C}(a_r, q) & \text{tie with } m \text{ others} \end{cases} \tag{6.1}$$

where a_r is the level of escalation at which the contest was decided, a_q the level to which the winner was willing to escalate, and $\lambda(q) \in [0,1]$ and is absolutely continuous. $U(a)$ is assumed to satisfy $U'(a) \leq 0$ and $U(a) > 0$ for all a and is included to represent the possibility that the value of the resource contested may decrease with level of escalation (Bishop & Canning 1978). Note that the OICG corresponds to the case $\lambda(q) = 0$ for all q, and the WOA is the case $\lambda(q) = 1$ for all q.

Generalization 2: Consider the best of n game for which the payoffs are given by:

$$\text{Payoff} = \begin{cases} -\hat{C}(a_q, q) & \text{lose} \\ U(a_r)V(q) - \hat{C}(\rho(a_r, a_q, q), q) & \text{win} \\ U(a_r)V(q)/(m+1) - \hat{C}(a_r, q) & \text{tie with } m \text{ others} \end{cases} \tag{6.2}$$

where $a_r \leq \rho(a_r, a_q, q) \leq a_q$ whenever $a_r \leq a_q$ and $\rho(a_r, a_q, q) = a_q$ whenever $a_r \geq a_q$. All other variables are as in Generalization 1.

The condition on U' assumed in the generalizations is more stringent than it needs to be. It may be replaced by the weaker condition $U'(a) < C_1(a, q_{\max})/V(q_{\max})$ for all a. This can be seen either by close inspection of the proof of the proposition below, or by the following intuition: the reason U' cannot be too great is that if the value of the resource increased at a rate faster than the rate of costs being incurred by some individuals, then these individuals would benefit by escalating, even if all their competitors had quit. This would lead to discontinuties in the ESS strategy and the results of section 2.2 would be inapplicable. Individuals of quality $q_{\max}$ have the lowest marginal escalation cost per unit of resource value, and thus if these individuals incur escalation costs, then so do all other individuals.

Proposition 6.1 *Assume* $\mathcal{A} = [a_{\min}, \infty)$ *and* $q_{\max} - q_{\min} < \infty$. *Further assume* *that F is a strictly increasing absolutely continuous function of q (continuity implies that f has no atoms of positive probability) and that f is bounded. Suppose that U, V and $\hat{C}$ are independent of A, V and $\hat{C}$ satisfy equations (2.2) and (2.8), that U is absolutely continuous, positive, and that $U'(a) \leq 0$ for all a and $V(q) > 0$ for all q.*

In the case of Generalization 1, if $\lambda'(q) \geq 0$ then there exists a unique ESS, $A^*(q)$, to the game defined by the payoffs given in (6.1). Further, A^* is absolutely continuous, $A^*(q_{\min}) = a_{\min}$, and satisfies the differential equation:

$$\frac{dA^*}{dq} = \frac{nU(A^*(q))V(q)F^{n-1}(q)f(q)}{(1-\lambda(q)F^n(q))\hat{C}_1(A^*(q),q) - U'(A^*(q))V(q)F^n(q)} \quad a.e. \qquad (6.3)$$

Similarly, in the case of Generalization 2, if $\rho(a_r, a_q, q)$ is absolutely continuous in a_q when $a_q > a_r$ and $\rho_2(a_r, a_q, q)$ is absolutely continuous in q when $a_q > a_r$ and, moreover, $\rho_2(a_r, a_q, q) \geq 0$ and $\rho_{23} \leq 0$ almost everywhere, then there exists a unique ESS, $A^*(q)$, to the game defined by the payoffs given in (6.2). Further, A^* is absolutely continuous, $A^*(q_{\min}) = a_{\min}$, and satisfies the differential equation:

$$\frac{dA^*}{dq} = \frac{nU(A^*(q))V(q)F^{n-1}(q)f(q)}{C_1(a,q) - U'(A^*(q))V(q)F^n(q)} \quad a.e. \qquad (6.4)$$

where C_1 is defined in the proof below.

Proof: A complete proof is first given for the first generalization under the assumption that $U(a) = 1$ for all a. $\mathcal{N}$ in this case is the same as in pool-comparison models of sexual selection. It is easy to check that $\mathcal{N} \in \mathcal{N}'(1-9)$, noting the fact that f is bounded in proving $\mathcal{N} \in \mathcal{N}'(7)$. The payoff, $P(A, a, q)$, to an individual of quality q playing a in a population which plays the strictly increasing function A is:

$$V(q)F^n(A^{-1}(a)) - (1-F^n(A^{-1}(a)))\hat{C}(a,q) - \int_{q_{\min}}^{A^{-1}(a)} (\lambda(q)\hat{C}(A(p),q) + (1-\lambda(q))\hat{C}(a,q)\frac{dF^n(p)}{dp} \cdot dp$$

where $A^{-1}(a)$ is defined as $\sup\{q; A(q) \leq a\}$. Identify $\mathcal{N}$ with F^n and C with:

$$(1-F^n(A^{-1}(a)))\hat{C}(a,q) + \int_{q_{\min}}^{A^{-1}(a)} (\lambda(q)\hat{C}(A(p),q) + (1-\lambda(q))\hat{C}(a,q)\frac{dF^n(p)}{dp} \cdot dp \qquad (6.5)$$

C satisfies equations (2.2) and (2.8) as $\hat{C}$ does. The result then follows from the proof of Proposition 2.1 if $\lambda(q_{\max}) < 1$.

For the case $\lambda(q_{\max}) = 1$, additional arguments are necessary. This is because the global existence of the solution to equation (6.3) is not guaranteed by Proposition A.3 as its denominator may go to zero as $q \to q_{\max}$. However, Proposition A.3 is satisfied for all intervals $[q_{\min}, q']$ whenever $q' < q_{\max}$, which gives uniqueness for all $q' < q_{\max}$.

As F is absolutely continuous, the set of individuals of quality $q_{\max}$ is of measure zero and, thus, the value of $A^*(q_{\max})$ is irrelevant to the uniqueness of A^* in the integral norm. However, it is worthwhile investigating $A^*(q_{\max})$, as doing so provides information about the rest of A^*. Set:

$$I(q) \overset{\text{def}}{=} \int_{q_{\min}}^{q} \frac{nF^{n-1}(q)f(q)}{1-\lambda(q)F^n(q)}$$

Further define:

$$\hat{C}_{\min}(a) \stackrel{\text{def}}{=} \frac{\hat{C}(a, q_{\min}) - \hat{C}(a_{\min}, q_{\min})}{V(q_{\min})}$$

and:

$$\hat{C}_{\max}(a) \stackrel{\text{def}}{=} \frac{\hat{C}(a, q_{\max}) - \hat{C}(a_{\min}, q_{\max})}{V(q_{\max})}$$

By solving bounding differential equations, it is easy to show that $A^*(q)$ is bounded above and below by $\hat{C}^{-1}_{\max}(I(q))$ and $\hat{C}^{-1}_{\min}(I(q))$ respectively.

Given that $\hat{C}_1 \geq \kappa$, this implies that if C is finite for all $q \in Q$ and finite a, then $A^*(q_{\max}) = \infty$ if and only if $I(q_{\max}) = \infty$. This is the case if $\lambda(q) = 1$ for some interval $[q, q_{\max}]$. Note that in the case of the WOA, $\lambda(q) = 1$ for all q and therefore in the case of the WOA, $A^*(q_{\max})$ is any a for which $C(a, q_{\max}) = \infty$.

The general case, in which U may be any function satisfying $U'(a) \leq 0$, follows from the above analysis after expanding and rearranging the payoff function:

$$P(A, a, q) = U(a_{\min})V(q)N(A, a) - [C(a, q) + (U(a_{\min}) - U(a))V(q)N(A, a)]$$

and replacing C in Proposition 2.1 by the term in square brackets. It is easy to check that this bracketed term satisfies all the relevant conditions as $U'(a) \leq 0$.

Generalization 2 follows in much the same way as Generalization 1, except:

$$C(a, q) = \int_Q \hat{C}(\rho(A(p), a, q), q)\frac{dF^n(p)}{dp} \cdot dp$$

and:

$$C_1(a, q) = (1 - F^n(A^{-1}(a))C_1(a, q) + \int_{q_{\min}}^{A^{-1}(a)} C_1(\rho(A(p), a, q), q)\rho_2(A(p), a, q)\frac{dF^n(p)}{dp} \cdot dp$$

Note that the integral of a function of A is used in the differential equation defining the equilibrium. Because of this, equation (6.4) does not satisfy the conditions of Proposition A.1 as it is stated. However, the statement of Proposition A.1 may be relaxed to encompass Generalization 2 with only trivial modifications of its proof. □

Setting $n = 1$ and $\lambda(q) = 1$ for all q and solving the differential equation, shows that this result is in agreement with the result presented without proof by Bishop et al. (1978, p385) for the continuous WOA with random rewards. Thus it may be viewed as an extension of this result. In particular, it gives results for more than two players and may also take account of the value of the resource depreciating with time (see section 3 of Bishop & Canning 1978).

Although the second generalization of the WOA and OICG is more comprehensive than the first generalization, Generalization 1 provides a convenient parameterization that has the WOA and OICG as its end points. Set $\lambda(q)$ constant for all q and $U(a) = 1$, then the first order condition, equation (6.3), becomes:

$$\frac{dA^*}{dq} = \frac{nV(q)F^{n-1}(q)f(q)}{(1 - \lambda F^n(q))\hat{C}_1(A^*(q), q)} \quad \text{a.e.} \tag{6.6}$$

When $\lambda = 0$ equation (6.6) is the same as the equation for the Nash equilibrium for the continuous OICG, and when $\lambda = 1$ we have the usual WOA equation.

6.1.3 Bounded Escalation and Error Prone War of Attritions

Clearly, the above arguments may be extended to the case of bounded advertising by the arguments in section 4.2 and to error-prone escalation by sections 2.4, 4.1 and 5.

6.1.4 The Limits of the Analysis

It has been claimed (e.g. Haigh & Rose 1980) that the ESSs of WOA-like models in which individuals value resources differently and perhaps pay different costs for escalating, differ radically from those in which individuals pay the same costs of escalation and value resources identically. Proposition 6.1 shows that the difference between these situations is only cosmetic.

Setting $n = 1$ and assuming V and C_1 are constant we see that equation (6.3) gives the usual WOA result (Maynard-Smith & Price 1973), if $A(q)$ is interpreted as the level of escalation by which $F(q)$ of the population will have ceased escalating. This is hardly surprising (consider V constant and taking limit $C_{12} \to 0$). However, the above proposition is not a proof of the standard WOA results, as equation (2.2) is not satisfied at the limit. Nevertheless, as P is continuous in C, Proposition 6.1 does imply that the solution to the relevant differential condition is an SNE (i.e. a Nash equilibrium). An application of Proposition 4.3 shows that this limit distribution of levels of escalation is the only possible SNE.

The ordering imposed by equation (2.2) on individuals quitting levels of escalation agrees with the discrete condition appearing in Bishop et al. (1978; Hammerstein & Parker 1982). Furthermore, the form of the ESS of Bishop et al. (1978) in the case in which individuals' valuations of resources take one of a finite number of values, may be obtained by applying equation (6.3) to:

$$\begin{aligned} n &= 1 \\ C(a,q) &= a \\ V(q) &= V_i \quad \text{if } F(q) \in \left[\sum_{j=1}^{i-1} p_i, \sum_{j=1}^{i} p_i\right) \end{aligned}$$

where:

$$V_{i-1} < V_i$$

•

Note that the result can be trivially extended to countable numbers of valuations.

A more subtle reason why the standard WOA result should not be expected to follow from the analysis contained in this section, is that the ESS of the standard WOA only satisfies the second order condition for an ESS; to first order it is only a Nash equilibrium (i.e. an SNE). The definition of ESS used here does not consider second order conditions, as this requires more information about the structure of the game than the first order condition. As suggested by the above analysis, to first order the OICG and WOA are almost indistinguishable; they both have Nash equilibria that satisfy equation (6.3). One has an ESS and the other does not because of second order considerations.

If the limitation of the above analysis was removed, that is, if we assumed more about the game's structure so that second order conditions could be obtained, then it would be reasonable to expect that a similar analysis would give very general results about the WOA. This turns out to be the case, but as it requires different interpretations of some of the variables used, and a reasonably lengthy mathematical diversion, it is not included here. As indicated by Proposition 4.3the ESS distributions of quitting levels of escalation turn out to be the same as those implied by equation (6.3), except that only weak inequality is assumed in equation (2.2). In particular, the ESS distribution of quitting times for individuals involved in a WOA between $n + 1$ identical players is given by:

$$\text{`Expected Proportion Ceased Escalating by } a\text{'} = \left(1 - \frac{V}{C_1} e^{-\frac{C_1}{V}(a - a_{\min})}\right)^{\frac{1}{n}}$$

Proofs of these and further results are in preparation (Siller manuscript in prep.).

6.1.5 Asymmetries, Assessment, and Variable Aggression

Turner & Huntingford (1986) have investigated agonistic contests between Mozambique mouthbrooders (*Oreochromis mossambicus*), a cichilid fish. Interestingly, the distribution of quitting times was nearly a negative exponential, the result predicted by the standard WOA. However, size was an excellent predictor of the contest outcome. The above model shows that these results are not enough to show that individuals are assessing each other; they could equally result from an error- prone WOA with q parameterizing fish length (see above and sections 4.1 and 5.4). Further evidence is required to show that assessment is occuring. Most theoretical analyses suggest that when assessment is occurring contest length or intensity should be greater the more similar a pair of contestants (Parker 1974; Parker & Rubenstein 1981; Enquist & Leimar 1983). Contest intensity was found to vary by Turner & Huntingford in the way predicted (see also Parker & Thompson 1980; Sigurjónsdóttir & Parker 1981).

Maynard-Smith & Harper (1988) have investigated the evolution of aggression. In particular, they used the WOA to suggest that it is possible for a population showing variability in aggression to be in an evolutionary stable state and this variation to be used to resolve contests. The above model extends their result. It states that variability in aggression should be correlated with an individuals ability to bear the costs of being aggressive, or valuation of resources.

6.2 Grafen 1990a

6.2.1 Grafen 1990a is a special case of Proposition 2.3

As adumbrated in section 2.2, Grafen's model of the strategic handicap principle is encompassed by Case 2 of Proposition 2.3. Here, it is shown how to translate Grafen's paper into the notation used in section 2. Familiarity with Grafen's (1990a) notation is assumed, but a key for translating notation between the two papers is provided in Table 2.

Technical differences: There are a few minor technical differences between Grafen (1990a) and Proposition 2.3:

Grafen	Siller
$G(q)$	$F(A,q)$
$\alpha(q,a)$	$S(A,a,q)$
1	$V^p(q)$
$z(q)$	$V^q(q)$
$Z(a)$	$\int_{A^{-1}(a)} V^q(q)\cdot dq$
$\mu\int_t U(t;D_1;A_1)m(t)D_1[A_2(q),t]\cdot dt$	$N(A_1,A_2(q))$
$\phi_M(A_2;A_1,D_2)$	$\int_{\mathcal{Q}} P(A_1,A_2(q),q)f(q)\cdot dq$
$K(q)$	$V^p(q)N^s(A,A(q))$
0	a_{min}
Q	$\mathcal{Q}$

Table 2: *Key to translation between Grafen (1990a) and the model solved in Proposition 2.3. Some properties of 'equivalents' differ slightly, as noted in the text. Notation not listed from either model is either irrelevant to one model, or has no direct equivalent.*

1. In Proposition 2.3 it is assumed that S may be a function of the population strategy, A. This was assumed so that situations in which the cost of a signal was relative to the population signalling strategy could be represented. Grafen makes the more restrictive assumption that α is dependent on the absolute value of advertising only.

2. In Proposition 2.3 it is assumed that $S(A,a,q)$ is differentiable in a and that this derivative is negative wherever $S \neq 0$, and that S_2/S is strictly increasing in q wherever $S \neq 0$. Grafen assumes that α is absolutely continuous and strictly decreasing in a, and:

$$q_1 < q_2 \text{ and } a_1 < a_2 \text{ implies } \frac{\alpha(q_1,a_2)}{\alpha(q_1,a_1)} < \frac{\alpha(q_2,a_2)}{\alpha(q_2,a_1)} \tag{6.7}$$

   That the condition on S_2/S implies equation (6.7) may be seen by taking the logarithm of equation (6.7) (the inequality is unaffected as the logarithm is a monotonic transformation) and then noting that S_2/S is the logarithmic derivative of S.

3. In Proposition 2.3 it is assumed that S/S_2 is Lipschitz in a. Grafen makes no similar or equivalent assumption about α.

4. Grafen's condition $\lim_{a\to\infty}\alpha(q_{\mathrm{max}},a) < K_{\mathrm{min}}/K_{\mathrm{max}}$ is replaced by the slightly weaker condition given by equation (2.15). Note that in Grafen's paper, $\alpha(q_{\mathrm{max}},0) = 1$ whilst the equivalent for S is not assumed.

5. Grafen assumes that α is absolutely continuous and strictly increasing in q. No such assumption is necessary in Proposition 2.3. All that is required is that $S(A,a,q_2) = 0$ implies that $S(A,a,q_1) = 0$ for all $q_1 \leq q_2$.

6. Grafen assumes that females infer the quality of males bearing a signal that is not usually seen in the population via local flat extrapolation (Grafen 1990a, p494). Local flat extrapolation does not assume a preferred direction, as is done here.

In general, the conditons in Proposition 2.3 are weaker than Grafen's conditions with two exceptions. First, α is only assumed to be absolutely continuous; and second, that Grafen does not assume that $1/\alpha^2$ is Lipschitz in a (where α^2 is the logarithmic derivative of α with respect to q).

It is assumed here that S_2 existed wherever $S \neq 0$ for the technical convenience of being able to use pointwise equilibrium conditons such as PBR and PNE. This has allowed an avoidance of much unnecessary circumlocution—but the results obtained in section 2 will still hold under Grafen's condition.

On the other hand, not assuming or proving that $1/\alpha^2$ is Lipschitz in a is a flaw in Grafen's model. In the proof of Grafen's Lemma 5 (Grafen 1990a, p507-9), he assumes that a differential equation (Grafen 1990a, equation A4.3) defines the best advertising strategy uniquely on regions where the equation is defined. This assertion is not true in general, but assuming that $1/\alpha^2$ is Lipschitz in a is enough to guarantee the result.

With these technical considerations in mind, the following result holds:

Proposition 6.2 *Proposition 2.3 section 3.2 implies that there exists at least one signalling ESS to the model constructed in Grafen (1990a).*

Sketch of Proof: The proof consists of showing that Grafen's model satisfies the conditions of Case 2 of Proposition 2.3, if the conditions on α are slightly altered as outlined in the previous list. Note that Grafen's, population genetics derived, necessary conditions for invasibility equate with the definition of an SNE, and that his sufficient conditions equate with the definition of an ESS used here.

The equivalent of N^s in Grafen's notation is $K(q)$ (which is a function of A). Grafen shows in his Lemma 5 that there exists a time before the end of the breeding season after which a female which has not mated should accept any male she encounters. He then shows that this implies that even the lowest quality male obtains at least $K_{\min} > 0$ reproductive success if he survives to the breeding season. This condition is important in Grafen's model, for the same reason as it is important to assume that at least some females do not discriminate between males in the model of section 5.3: for if the lowest quality males have zero fitness when signalling honestly, they have nothing to lose by signalling dishonestly.

It may be seen from its definition that $K(q)$ is continuous in A, under the assumption that females can discriminate between male qualities that advertise at the same level. Lemma 7 (or direct calculation assuming the derivative of $\psi^*(t)/m(t)$ using Lemma 1) proves that $K(q)$ is continuous in q provided $m(t)$ is not exponential in form on any interval. To show the existence of an ESS using the mechanics of Proposition 2.3, we do not need K to satisfy any other properties (these 'excess' assumptions, and the associated calculations, were used in the main text to show that the only ESSs were of a certain form).

The relevant space of female strategies is the set of decreasing functions:

$$\psi : [0,T] \rightarrow [0, z(q_{\max})(\sup\{m(t)\}) + 1]$$

which are zero on $[t', T]$, where t' is defined on p496 of Grafen (1990a). Denote this space by $\mathcal{D}$.

After making the substitutions outlined in Table 2, it is clear, by Lemma 2.1 of this paper, that we may assume that A is increasing when considering the female strategy if the logarithmic transformation is valid. The space of male advertising strategies that needs to be considered is the set of increasing functions:

$$A : [q_{\min}, q_{\max}] \rightarrow [0, B]$$

where B is defined on p497 of Grafen (1990a). Denote this space by $\mathcal{S}$.

Using the appropriate substitutions from Table 2, set:

$$(M_{\mathcal{D}} \times M_{\mathcal{S}}) \circ \Delta : \{\psi, A\} \mapsto \{v(A), M(A, v(A))\}$$

where $M(A, v(A))$ is defined by equation (2.17), with $N^s \equiv K$ determined by $v(A)$ ($v(A)$ is defined by equations SE(1-3) of Grafen (1990a); v is continuous in A)) and Δ the duplication map (see section 3.2). Clearly, $(M_{\mathcal{D}} \times M_{\mathcal{S}}) \circ \Delta$ is continuous and maps $\mathcal{D} \times \mathcal{S}$ into itself, and $\mathcal{D} \times \mathcal{S}$ is compact and convex. Schauder's Theorem then implies the existence of a fixed point. The fact that $K(q)$ is strictly increasing and absolutely continuous implies $K'(q)$ exists almost everywhere and is positive almost everywhere. In turn this implies that the fixed point must be strictly increasing by the definition of M. Thus, the assumption of using equations pertaining to a splitting equilibrium is validated.

□

It should be noted that Grafen's equation (A4.3) which defines the male signalling strategy, is the same as equation (2.17), as expected. It should be noted that the entirety of Grafen's result has not been proven. Grafen's complete result, with the exception of the error outlined below, would follow if it were shown that his equivalent of 'N' satisfies $N(1-5, 7-10)$. These calculations have not been conducted here as it would require a lot of space, for little gain.

6.2.2 An error in Grafen's proof of uniqueness

In his model of sexual selection, Grafen (1990a) claims that there are precisely two ESSs to his model. The first is a non-signalling equilibrium, where females do not discriminate between males, and males do not advertise. The second is a unique splitting signalling equilibrium, in which males advertise as an increasing function of quality and females discriminate between them. The proof of uniqueness of the second equilibrium is contained in Lemma 9 (p513-514) of the paper. There are a few mistakes in signs contained in the proof of this lemma, and once corrected, the uniqueness result no longer follows. The following is a repetition of the relevant section of the proof with corrections using Grafen's notation, starting from the ninth line of p514:

Taking logs before differentiating, we obtain:

$$\frac{L_i'(A_i(q))}{L_i(A_i(q))} = -\alpha^2(q, A_i(q)),$$

and integrating with respect to a we obtain:

$$L_i(a) \propto \exp\left\{-\int_0^a \alpha^2[A_i^{-1}(a'), a']da'\right\}, \text{ for } a \in [0, A_i(q_{\max})].$$

Let $n_i(q,a)$ be the derivative with respect to a of $\ln[\alpha(q,a)L_i(a)]$ for $i = 1, 2$, then:

$$\begin{aligned} n_1(q,a) &= \alpha^2(q,a) - \alpha^2(A_1^{-1}a, a) \\ n_2(q,a) &= \alpha^2(q,a) - \alpha^2(A_2^{-1}a, a). \end{aligned}$$

Consider some value of q where, without loss of generality, $A_1(q) < A_2(q)$. Because the A_i are strictly increasing and continuous, it follows that $A_1^{-1}A_1(q) > A_2^{-1}A_1(q)$. We also know that $\alpha^2(q,a)$ is increasing in q, so that:

$$\alpha^2[A_1^{-1}A_1(q), a] > \alpha^2[A_2^{-1}A_1(q), a].$$

It follows that:

$$n_1[q, A_1(q)] < n_2[q, A_1(q)],$$

and by definition $n_1[q, A_1(q)] = 0$. Hence:

$$n_2[q, A_1(q)] > 0.$$

It is at this point that Grafen's proof fails. In his paper, the last inequality was reversed, which allowed him to obtain a contradiction observing the proof of Lemma 8 which showed that for $a < A_2(q)$, $n_2(q,a) > 0$. This is no longer a contradiction, but is in agreement with the last inequality, which should not be surprising, as the construction involved in Lemma 9 is an attempt to get something from nothing.

In conclusion, Grafen has not shown that there is a *unique* strategic handicap signalling ESS for his model. It may turn out that his assertion is true for his particular model; intuitively, it seems reasonable. However, the method of constructing models with multiple ESSs outlined in section 2.5 shows that unique signalling ESSs will not necessarily be the case.

6.3 Grafen 1990b

6.3.1 Two Errors in Grafen's Proof of Existence

There are two errors in the proof of the existence of a solution in the basic ESS model outlined in Appendix 2 of (Grafen 1990b), which also carry over into Appendix 4. These problems are trivial to rectify, but their existence has potential biological significance. Grafen's notation is used in this section without explanation; his definitions are easy to find in the original paper.

The first problem, which has little bearing on the proof of the result as it may be circumvented, is that the differential equation:

$$\begin{aligned} P^{*\prime}(a) &= -\frac{w_1[a, P^*(a), P^*(a)]}{w_2[a, P^*(a), P^*(a)]} && (6.8) \\ P^*(a_{\min}) &= q_{\min} && (6.9) \end{aligned}$$

may not have a solution for all advertising levels $a \in [a_{\min}, \infty)$, due to P^* asymptoting at some value of a. Consider the function:

$$w(a,p,q) = p + \exp(-a(1+q^2)).$$

It satisfies all conditions prescribed, namely: $w_1 < 0$, $w_2 > 0$, and:

$$\frac{\partial}{\partial q}\left(\frac{w_1(a,p,q)}{w_2(a,p,q)}\right) > 0,$$

for all a, p, q. Yet, it is not true that a solution exists to the system equations (6.8) and (6.9) over the entire interval $[a_{\min}, \infty)$, as the solution in a suitably small neighbourhood of $a_{\min}$ is given by:

$$P^*(a) = \tan(a - a_{\min} + \arctan(q_{\min}))$$

which 'blows up' at $\pi/2 + a_{\min} - \arctan(q_{\min})$.

The second problem, which is in a sense the inverse of the first, is more critical. Grafen defines the ESS advertising function $A^*(q)$ to be the right inverse of the perception function P^*, but this may not exist if a asypmtotes for some value of P^* Consider:

$$w(a,p,q) = p + \frac{(\exp(q_{\min} - q) + 1)}{a - a_{\min} + 1} + q - q_{\min}.$$

This function satisfies all the given conditions, as well as satisfying the intuitive condition $w_3 \geq 0$ for the range of values of q that we are considering. However, upon solving equations (6.8) and (6.9), we see that the solution is given implicitly by:

$$(P^* - q_{\min})\ln(\exp(q_{\min} - P^*) + 1) = 1 + \ln 2 - \frac{1}{a - a_{\min} + 1}$$

which asymptotes at the value of P^* given by:

$$(P^* - q_{\min})\ln(\exp(q_{\min} - P^*) + 1) = 1 + \ln 2. \tag{6.10}$$

This solution exists by the intermediate value theorem and is unique on $P^* \in [q_{\min}, \infty)$. Perhaps more simply, as the numerator of $-w_1/w_2$ is bounded above by 2, we may simply note that:

$$q_{\min} \leq P^* \leq q_{\min} + 2.$$

Thus, as $a \geq a_{\min}$, if the range of qualities extant in the population is large enough, then no right inverse exists over the entire set of qualities. Intuitively this result is the situation where individuals of high quality cannot advertise enough to distinguish themselves from individuals of lower quality. In other words, when signalling is cheap enough, the optimal strategy for some individuals in the population is to produce a signal, a, of infinite magnitude. Of course, this does not make biological sense if the signal is a physical magnitude, such as the length of a tail or the loudness of a call—extreme exaggerations of such signals will not be cheap. However, there are circumstances in which a signal level of ∞ can be interpreted sensibly by rescaling the a-axis. For instance, suppose that the signal was the proportion of an organism that is coloured black, the cost of the signal being, say, the energetic or survival cost of producing or obtaining the pigment, or an increased predation risk due to greater visibility. The proportion of an individual coloured, $c \in [0, 1]$ can then be related to an interval of infinite length $[a_{\min}, \infty]$ by a transformation such as:

$$c = 1 - \frac{1}{a - a_{\min} + 1}$$

Thus, $a = \infty$ is, in this case, the circumstance in which the signalling organism has produced the maximal possible signal—once the entire organism has been coloured the deepest black there is no further possibility of increasing the signal.

This situation is dealt with by the model solved in Proposition 4.4, and the result shows that an ESS may still exist, but it is qualitatively different from the ESSs previously envisioned.

6.3.2 Sufficient Conditions for Existence

It is a sufficient condition for an inverse function to exist, no matter what the range of qualities, that:

$$-w_1/w_2 \geq \frac{\epsilon_1}{a - a_{\min} + \epsilon_2}, \quad \epsilon_1, \epsilon_2 > 0$$

for all a, p, q. That is, either $-w_1/w_2$ is bounded away from 0, or if it does go to zero in the limit as a tends to infinity, it must go slow enough.

6.4 Computational Errors: Grafen & Johnstone 1993, Johnstone 1994, 1996

Proposition 2.4, together with section 4.1, provide the continuous analogue of the discrete computational models of Grafen & Johnstone (1993; Johnstone 1994, 1996). These authors suggest, from the results of their computer simulations, that error-prone handicap signals may have some features that are not seen in models of handicap signals which are error-free. As Proposition 2.4 is not specific to error-prone signals, it may be concluded that their results are not due to the error in the signal *per se*. In any case, some of their conclusions are supported by the analytical treatment presented in Proposition 2.4. However, certain of their results seem to arise from the particular form of cost functions that they assumed, and others from the discreteness assumed to facilitate computation. (To be fair, the authors did dwell on these possibilities.)

> **Initial Flats:** In almost all the computer simulations reported, signalling ESSs exhibited an 'initial flat' In all simulations, individuals of the lower qualities advertised at the lowest possible level. These are not a necessary features of error-prone signals, as demonstrated by Ex.2, Ex.3 and Ex.6 of section 2.5 (which also show that the lowest quality individuals need not advertise at the lowest level possible; see also section 7.1). The simulations had this feature because of the choice of functions representing the cost of advertising that were made; in particular, the cost function of Johnstone (1994) had extremely large marginal costs of advertising for individuals of low quality (in fact infinite for the lowest qualities) relative to the benefits observed.
>
> In the model presented by Grafen & Johnstone (1993), fitness is given by:
>
> $$r \ln(i + i_0)(a - a_0) \ln\left(\frac{q - q_0}{1.01(q_{\max} - q_0)}\right)$$

where $i_0 \geq (1 - q_{\text{min}})$, $q_0 \leq q_{\text{min}}$. Given the error distribution that they have chosen, it may be shown that:

$$\frac{di}{da} \leq \frac{q_{\text{max}} - q_{\text{min}}}{v}$$

where v is a parameter related to the variance of the distribution. Calculation then shows that individuals of quality q must advertise at a_0 if:

$$q < q_0 + 1.01(q_{\text{max}} - q_{\text{min}}) \exp\left(\frac{q_{\text{min}} - q_{\text{max}}}{v}\right)$$

This analysis shows that the possible behaviour of the model can be limited by a poor choice of parameters. It is impossible to analyse Grafen & Johnstone (1993) further, as they did not provide the ranges of parameters from which they drew their conclusions.

Grafen & Johnstone (1993) also suggested that these initial flats were longer the greater the perceptual error. Proposition 4.1 shows that this is true in the limit as variance goes to infinity. The proof of Proposition 4.1 suggests that this may be approximately true at less extreme variances; for a given A, increasing error in perception, reduces the maximum marginal benefit obtainable. Similarly, for a given A, increasing error in perception increases the fitness of individuals advertising at a_{min}. However, counter examples do exist.

Jump from Initial Flat to Signalling: The simulations suggested that ESSs jump from the initial flat to a level approximately equal to a level of signalling similar to that expected if there was no error. As stated above, Ex.3 of section 2.5 shows that this flat need not exist and Ex.4 shows that even if it does exist, there need not be a discontinuity.

Non-Zero Advertising Levels are of Similar Magnitude: It has also been suggested that the advertising strategies are roughly independent of the amount of error in the signals after the initial flat. This is not true in general, and it is clear that the method of constructing examples given in section 2.5 can be used to provide counter-examples.

Consider an additive payoff situation with $V(q) = 1$. Suppose that error in perception of the signal is normally distributed, and that females use a best-of-n strategy, where n is assumed to be fixed for the moment. Further, consider a linear signalling relationship A, for which $A(q_{\text{min}}) = a_{\text{min}}$. The idea is to construct the signalling cost function C so that A is an ESS and then compare A with the error-free ESS, A^*, arising from the same cost function.

In particular, choose some particular variance error in perception, σ^2 and, for $a \in [a_{\text{min}}, A(q_{\text{max}})]$, set:

$$C_1(a,q) = \frac{\partial N(A,a,\sigma)}{\partial a}\left(1 + \frac{A^{-1}(a) - q}{q_{\text{max}} - q_{\text{min}} + d_1}\right)$$

where $N(A,a,\sigma)$ is the payoff for signal of level a in a population signalling at $A(q)$ and error in perception by receivers of variance σ^2 For $a > A(q_{\text{max}})$ set:

$$C_1(a,q) = \frac{\partial N(A,a,\sigma)}{\partial a}\left(1 + \frac{q_{\text{max}} - q + d_2}{q_{\text{max}} - q_{\text{min}} + d_1}\right)$$

where d_1 and d_2 are both greater than zero.

As d_1 can be arbitrarily large and d_2 arbitrarily small, the difference between $C_1(a, q_{\min})$ and $C_1(a, q_{\max})$ can be made arbitrarily small. In particular:

$$\sup_{a \in \mathcal{A}} (C_1(a, q_{\min}) - C_1(a, q_{\max}))$$

may be arbitrarily small. Moreover, by increasing error variance, σ^2, it is clearly possible to lower $N_2(A, a, \sigma)$ below any given value. In particular, it is clear that N_2 is bounded above and below for each σ and that:

$$\lim_{\sigma \to \infty} \sup N_2(A, a, \sigma) = 0$$

Thus, we may construct a model for which C_1 is bounded above by a $\epsilon > 0$ which is arbitrarily small.

In summary, it is possible to construct a best-of-n signalling game to which there exists a signalling ESS, A, which has arbitrarily small but non-zero slope (i.e. there is no initial flat) and for which C_1 is bounded above by some arbitrarily small constant, $\epsilon > 0$.

The ESS, A^*, of the equivalent signalling game with no error in perception is, by section 5.2, given by:

$$\frac{dA^*}{dq} = \frac{(n-1)f(q)F^{n-2}(q)}{C_1(A^*(q), q)}$$

As C_1 is bounded above by ϵ, A^* is bounded below by:

$$\frac{dA^\circ}{dq} = \frac{(n-1)f(q)F^{n-2}(q)}{\epsilon}$$

Thus, the ESSs to the error-free signalling situation, A^*, and the error-prone signalling situation A, can both be strictly increasing everywhere yet arbitrarily different. Therefore, the claim that non-zero signalling levels are roughly the same, regardless of error, can be seen not to be true in general.

It should be noted that no consideration was made of the effect of differing payoffs to females choosing from n in the error-prone and error-free situations. In particular, females receive better quality males when picking the best of n males in the error-free situation. Thus, if the complete model of receiver/signaller interactions was considered, the difference between A^* and A would be further exaggerated as the ESS female strategy will be to pick from larger samples in the error-free case. (Note that the female costs can be constructed so that they choose from $n > 1$ in the error-prone case; see section 9.7 for an example.)

It should not be concluded from the above example that error-prone signalling ESSs depart less from $a_{\min}$ than the ESSs to the equivalent error-free situation.

Secondary Flats: Proposition 2.4 shows that, apart from the possiblility of an initial flat (and in the case of bounded advertising, a final flat), an ESS must be strictly increasing. As the error distributions used in Grafen & Johnstone (1993) and Johnstone (1994) have compact support, we cannot use the conditions given in section 4.1.1 to show that their models satisfy the conditions of Proposition 2.4. It is possible to show that there can be no secondary flats in the continuous analogues of their models by analysis, but this would require a lengthy divergence. However, it can be seen directly that the continuous analogues of the ESSs that they arrive at computationally are such that the associated N is strictly increasing over the support of the set of values of perceived levels of signalling in the population. Thus, by part [2] of the proof of Proposition 2.4, the pointwise best response (PBR) to Grafen and Johnstone's computational ESSs must be strictly increasing. That is, the flats in the ESSs that they have obtained are due to the coarseness of the discretization used in their model.

These secondary flats would disappear in these computational models if a fine enough advertising level grid was used, regardless of the amount of error in signalling. (To be precise, for any given model, an upper bound on the length of a secondary flat may be calculated for a given partitioning of signalling. This length can be shown to go to zero as the maximum width of partitions of signalling level goes to zero, whilst holding the quality partition fixed. In discrete models, secondary flats can always occur if quality is partitioned much more finely than signalling, but even with this consideration, the absolute length of these flats must decrease with finer signalling partitions.)

Thus, Johnstone's (1994) hypothesis that error in signalling provides an explanation for 'all or nothing' displays, seems rather unlikely.

The analystical result that signalling equilibria must be strictly increasing in quality, except on boundaries, brings into question the implementation of the model described in Grafen & Johnstone (1993). In Figure 1 of this paper, Grafen & Johnstone provide examples of signalling equilibria obtained by their computational model. In this model they described signalling as a continuous variable, whilst quality was assumed to be discrete. The argument [2] of Proposition 2.4, may be used to show that the secondary flat observed in Figure 1 of Grafen & Johnstone (1993) cannot arise if signalling is treated as a continuous variable. It appears that the error function was discretized in the computational model. There does not appear to be any reason for this, as it is possible to obtain a simple funcitonal form for the cumulative distribution function of the error function that they used. The only discreteness that would appear in this case would be that due to rounding error, which is of such a small order of magnititude that it could not cause secondary flats.

Of course, there is the possibility that, although error-prone signalling cannot give rise to secondary flats, it may regularly give rise to secondary pseudo-flats. That is, the ESS could be step-like, with alternating sections of gentle and steep gradients. However, apart from Johnstone's (1994) numerical results there does not appear to be a reason to suspect this. It is certainly a question that warrants further investigation.

Concrete Models of Receiver Behaviour: A noticable difference between Johnstone's (1994, 1996) two papers is that in the earlier paper there appeared to be multiple signal equilibria for a given set of circumstances, whilst in the model of the latter paper Johnstone found only one combined signaller and receiver ESS. He hypothesized that this resulted from the incorporation of a concrete model of receiver choice in the model analysed in the second paper. The following simple example shows that there can be multiple signalling ESSs to a model which incorporates a concrete model of receiver behaviour.

The example given here is basically a two quality version of the model in Johnstone (1996). The underlying idea can be extended to a continuous distribution of qualities, but the extra calculation only serves to obscure the example. Suppose that the population of signallers is divided equally between two qualities, q_1 and q_2. All receivers are assumed to be identical. The value to a receiver choosing a signaller of quality q_i is assumed to be V_i, and similarly the value of being chosen to a signaller of quality q_i is V_i. It is assumed that $V_2 > V_1$. Signallers can choose to send signals of levels ranging over $[a_{\min}, \infty)$. Signal reception is error-prone, and the distribution of error of a signal of level a is assumed to be the flat distribution over $[a - w, a + w]$. It is possible for a signal to be perceived as being of a level lower than $a_{\min}$. Receivers may choose the signaller that they are currently sampling, or they may sample another signaller at a cost k where it is assumed:

$$\frac{(1-z)^2}{1+z}\frac{V_1+V_2}{2} < k < \frac{V_2-V_1}{2} \tag{6.11}$$

where $z < 1$ is an arbitrary factor chosen so that the above inequality holds.

Assume that the cost of signalling at a level a to an individual of quality q_i, denoted $C(a, q_i)$ is given by:

$$C(a, q_i) = \begin{cases} \frac{V_1(a-a_{\min})}{w} & q_i = q_1 \\ \frac{V_2(a-a_{\min})}{3w} & q_i = q_2 \end{cases}$$

I now claim that the strategy $A(q_1) = a_{\min}$, $A(q_2) = a_2$ is an ESS provided $a_2 - a_{\min} > 2wz$. As a_2 is somewhat arbitrary in this condition, there are multiple ESSs to the above signalling receiving game.

The first thing that must analysed is the female strategy. There are three possible conclusions that a receiver may draw from a signal:

1. If the perceived level of signal p is less than $a_2 - w$, then the signaller is of value V_1;
2. If the perceived level of signal lies in $[a_2 - w, a_{\min} + w]$, then there is an even chance that the signaller is of value V_1 or value V_2; or
3. If the perceived level of signal is greater than $a_{\min} + w$, then the signaller is of value V_2.

As the cost of sampling another signaller is independent of the number of signallers already sampled, and noting the Concorde fallacy (Dawkins & Carlisle 1976; Dawkins 1976), there are only three reasonable receiver strategies that need be considered:

1. Accept any signaller;
2. Only accept a signaller if it is perceived to signal at $a_2 - w$ or above; or
3. Only accept a signaller if it is perceived to signal above $a_{\min} + w$.

The expected fitness of a receiver playing strategy 1 is then $(V_1 + V_2)/2$. A receiver playing strategy 2 keeps sampling until it comes across a signaller signalling high enough. Noting the sum of a geometric series $p + p^2 + p^3 + \ldots = p/(1-p)$ if $0 \leq p < 1$ we see that the expected fitness of a receiver playing strategy 2 is:

$$\frac{V_2 + V_1(1 - \frac{a_2 - a_{\min}}{2w})}{2 - \frac{a_2 - a_{\min}}{2w}} - k\frac{a_2 - a_{\min}}{4w - a_2 + a_{\min}}$$

Similarly, a receiver playing strategy 3 can expect a payoff:

$$V_2 - k\frac{2w + a_2 - a_{\min}}{2w - a_2 + a_{\min}}$$

As $(a_2 - a_{\min})/2w \geq z$, a simple calculation shows that strategy 2 is the best receiver strategy.

All that is left to show is that the signallers strategy is an ESS. Clearly, we need only consider strategies between $a_{\min}$ and a_2. This is because it is assumed that individuals cannot signal below $a_{\min}$ and signalling above a_2 does not increase the chance that an individual is chosen by a receiver above that if the signaller signalled at a_2 (because receivers always choose signallers that are perceived to be signalling at $a_2 - w$ or above), but is more costly.

The fitness of a signaller of quality q_1 signalling at $a \in [a_{\min}, a_2]$ is then given by:

$$V_1\left(1 - \frac{a_2 - a}{2w}\right) - \frac{V_1(a - a_{\min})}{w}$$

which is maximized at $a = a_{\min}$ whilst the fitness of a signaller of quality q_2 signalling at $a \in [a_{\min}, a_2]$ is given by:

$$V_2\left(1 - \frac{a_2 - a}{2w}\right) - \frac{V_2(a - a_{\min})}{3w}$$

which is maximized at $a = a_2$. Hence the signalling strategy outlined above is an ESS provided $(a_2 - a_{\min})/2w \geq z$. Thus, multiple signalling ESSs exist in this model for a fixed set of parameters.

It should be noted that the analysis of the results of these three computational papers did not require the solving of an analytical model of error-prone signalling.

7 Biological Applications

7.1 Peacock Tails

One of the difficulties with previous strategic signalling models (e.g. Grafen 1990a,b; Godfray 1991; Grafen & Johnstone 1993; Johnstone 1994) is that they predict that the lowest quality individuals (or in the case of Godfray, the least needy individuals) should signal at the lowest possible level. As discussed in section 4.3, it is not necessarily the case that the 'lowest possible level of signalling' is no signal at all, but should be interpreted as the level of signal which is the least costly in terms of survival. However, even with this qualification, this does not match with common intuitions about the costliness of gross ornaments, such as a peacock's tail and colouring, which are developed by all adult males in a population.

It was observed in section 2.5 that, under the conditions of Proposition 2.4, there can exist strategic signalling equilibria, A^*, for which $A^*(q_{\min}) > a_{\min}$. Under what conditions should we expect the conditions of Proposition 2.4 to be satisfied, and given that they are satisfied, what further conditions are sufficient for an ESS to satisfy $A^*(q_{\min}) > a_{\min}$? Are these conditions then biologically reasonable?

Unfortunately, there is no single simple answer to such questions, and this is reflected in the comparative lack of rigour in the following analysis. However, it is possible to approach the question from the opposite direction, making biologically reasonable assumptions and then showing that we might expect the ESS to be of the form $A^*(q_{\min}) > a_{\min}$.

Let us restrict our attention to the case of sexual selection via exaggerated ornaments in a species without paternal care of young. The appropriate partition of fitness in this instance is a multiplicative one, say:

$$P(A, a, q) = V(q)N(A, a)S(A, a, q)$$

where N is some measure of the number and quality of matings obtained by a male per unit time, and S is a measure of his expected longevity. As remarked in section 5.3, if $N(A, a_{\min}) = 0$ then a low quality male has nothing to lose by advertising at a level higher than $a_{\min}$. It is conceivable that there might be a level a' below which females are unwilling to mate with a male. For instance, a female may need to be able to recognize the male to be of her species, or at least to be a sexually mature member of her species, as mating with a male of another species or an infertile immature male would be costly to her reproductive success. (Williams 1992). Making such a mating mistake could be more costly than not mating at all because, for example, brooding a nest of infertile eggs is likely to increase the mother's chance of mortality for no benefit.

The logarithmic transformation required to make the multiplicative model satisfy the conditions of Proposition 2.4 is not defined on any region on which $N(A, a) = 0$, so analysis further to that presented here would be required to treat this case fully.

The first order condition in Proposition 2.4 has the same signa as:

$$N_2(A, a)S(A, a, q) + N(A, a)S_2(A, a, q) \tag{7.1}$$

Fitness is increasing in a wherever equation (7.1) is positive. If most of the population is siganlling at a high level, then one would expect that N was small near $a_{\min}$, whilst S will be relatively high for a close to $a_{\min}$. In this case, equation (7.1) means that near $a_{\min}$, signallers will be willing to pay high marginal costs (i.e. S_2) for low marginal increases in mating success (i.e. N_2). This is the same as the Desperado Effect of Grafen (1987).

At an ESS, equation (7.1) must be zero for almost all q. Noting that the left hand summand is positive and may be interpreted roughly as the marginal increase in fitness due to mating success, and the right hand summand is negative and may be interpreted as the marginal decrease in fitness due to increased mortality, we can view an ESS as a balance between the two summands. This balance is 'promoted' if A has a reasonably gentle slope relative to the ratio of the width of error in perception relative to $q_{\max} - q_{\min}$. Similarly, a reduction in S increases the likelihood of A being an equilibrium. Both these factors would seem to be plausibly associated with a population which bears extremely exaggerated sexually selected traits, in which the difference between the most and least developed traits is significantly smaller than the difference between the least developed trait and the survival optimum level of development.

Regardless of the universal validity of the above argument, it is possible to construct specific models which have signalling ESSs which satisfy the condition of low relative versus absolute exaggeration. The general methods for doing this are sketched throughout this paper, in particular in section 2.5.

Of course, there are other explanations for the phenomenon described here: the Fisher process and the Epistatic Handicap Mechanism (chapters 9 and 10) also provide plausible explanations. However, the important point is that the observation of previous modellers (referenced above) that lowest quality individuals advertise at the lowest possible level, is only a modelling artefact, and not a limitation of strategic signalling descriptions.

7.2 Five Potential Explanations of Intrasexual Plumage Dimorphism

Johnstone (1994) has suggested that error in signalling may account for 'all or nothing' signals. Now, although the analysis of section 6.4 cannot refute this possibility, it is worthwhile considering some more biological explanations of this phenomena, as strategic signalling may easily give rise to qualitatively dimorphic signals without having to resort to mathematical peculiarities. Below, five plausible mechanisms are presented by which pseudo-discrete signalling might arise in a population of males with continuous distribution of qualities.

7.2.1 High Operational Sex Ratio

It is often the case that the operational sex ratio (Emlen & Oring 1977, Hammerstein & Parker 1987) is high, for example in the case of a lekking species, or a monogamous species in which the number of adult males is greater than the number of females (e.g. mallards, Cramp & Simmons 1977; Bellrose et al. 1961) or in which the number of breeding territories is much smaller than the number of males. *Ceteris paribus*, the 'extra' low quality males will not be able to pair with females. Assuming that the amount of uncertainty in the sex ratio and other stochastic factors are small, N to males would look roughly similar to the left graph of Fig 5. Assuming that the ESS is continous, this would induce a male advertising ESS that looked similar; i.e. a dimorphic ESS.

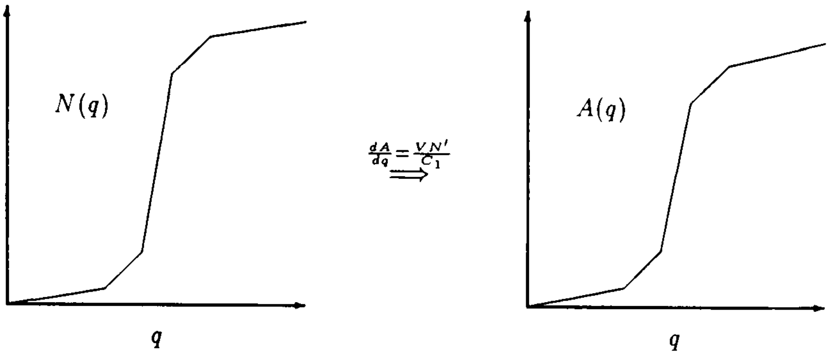

Figure 5: *Sigmoidal shaped N, in general, give rise to sigmoidal advertising ESSs, via the first order condition on ESSs.*

7.2.2 Distinct Classes of Females

Another possible explanation for signal dimorphism, not usually considered, is that there might be distinct classes of females. Consider a species of monogamous passerines in which the increase in the ability of females to raise a brood has a sharp increase between their first and second breeding season, relative to the increase (if any) between later seasons, perhaps due to experience or because first year females have not been able to store as many resources for the production of eggs due to part of the resources obtained in their first year being spent on their own growth. Assume that females increase their fitness by mating with males of high quality, and suppose that males can determine whether a female is a yearling or not, that they can only accept one female, and exert choice between them. A process of assortative mating will lead to the yearling females being paired with low quality males, and the older females all being paired with high quality males. Thus, if there are roughly equal numbers of males and females, and there is a proportion p of females breeding for the first time, one would expect a sharp increase in the male fitness function for males being perceived as being in the top $1 - p$ of male quality (see Fig.5). As the form of the male advertising ESS is largely determined by the rate of increase in fitness due to perceived quality, in this situation we should expect male advertisements to be dimorphic.

7.2.3 Distinct Classes of Males

The central concept behind the previous potential explanation was that N was a step function, or nearly so. A related possibility is that the population may be divided into almost discrete groups amongst which C is significantly different. For example, in a species with biparental care, successful raising of young may be dependent on learning, and the ability to raise young may differ significantly between those males who have raised or attempted to raise one brood, and those who have not attempted to raise a brood. In mathematical notation, V may differ significantly between the two groups of males. In a model with error-prone signalling this can easily lead to a pseudo-dimorphic equilibrium.

7.2.4 Upper Bound on Possible Signal

A fourth possibility that may lead to intrasexual signal dimorphism is the existence of an upper bound on the possible level of signalling. This result is contained in Proposition 4.4.

7.2.5 Female Sampling Tactics

The final possible explanation for intrasexual signal dimorphism that arises from this paper is that it may be due to female sampling tactics. This is discussed in relation to the 'one-step decision process' in section 5.5.

7.3 Honest Signalling of Future Parental Investment

It has been suggested that sexual selection might be supported by females choosing males for non- heritable traits, such as parental ability. Whilst this suggestion avoids some of the difficulties related to selection for 'good genes', it does have some problems of its own.

The case of male parental ability seems particularly problematic, as the female has to commit to a heavy investment in reproduction with her chosen male before the male has to return his 'promise' of being a good father. Once a female has made such an investment, it may be too late or too costly for her to abandon the clutch and start again with another male. Thus, the chosen male seems to be in a position of power. Once the female has invested in him, he can choose whichever strategy is best in terms of his fitness. Why should the 'promise' of being a good father be kept? There are, of course, numerous plausible answers to this question. Proposition 2.1 suggests one interesting answer:

Let q be an ordering on the amount of parental effort that males are willing to expend, high q representing a relatively large parental effort. Clearly, females would prefer to mate with males who are going to invest heavily in their offspring. Thus, because of assortative mating or some similar reason, we would expect $N(p)$ to be increasing in the perceived willingness of a male to invest, p. *Ceteris paribus*, males should wish to signal a willingness to invest heavily.

The details of why actual parental investment may differ between males shall not be dealt with here. Suppose that the cost of the parental signal is the same to all males, i.e. $C(a, q)$ is independent of q. Naïvely, one may expect that as there is no difference in signalling costs amongst males, there could be no separating ESS.

However, equation (2.2) also contains the term $V(q)$. In this case, the fitness of a brood of offspring might reasonably be assumed to be the product of the female's contribution, N, and some increasing function of actual paternal care, $V(q)$. Thus, although C is assumed to be independent of q, equation (2.2):

$$\frac{\partial}{\partial q}\left(\frac{C'(a)}{V(q)}\right) = \frac{-C'(a)V'(q)}{V^2(q)} < 0$$

is still satisfied if V is strictly increasing in q. Proposition 2.1 shows that there is a separating signalling ESS in such a situation. Therefore, honest signalling of actual future parental investment, by otherwise identical males, can be evolutionarily stable. At an ESS, a male who will only invest at a level q does worse by signalling that he will invest at some different level. This is because the payoff that the male receives is increasing, not only in his 'promised' investment, but also in his actual investment, which is equivalent to marginal costs being decreasing in actual investment.

7.4 Competition Between Relatives

The argument presented below is not an attempt to extend the generality of the results of chapter 2 to signalling/competitions between relatives. Such an analysis deserves more attention than can be given here, as there are many potential pitfalls associated with modelling inclusive fitness (Dawkins 1979; Grafen 1979, 1982, 1991). However, only simple modifications of the models of chapter 2 are needed to provide a confirmation of the basic intuition that competition amongst relatives should be cheaper than similar competition amongst unrelated individuals.

7.4.1 2-Player Pool-Comparison Games Between Relatives

For reasons that will shortly become apparent, it will initially be necessary to restrict attention to a pool-comparison model. First, consider the case when the competition is between two contestants only, with expected relatedness r The central idea is to find a population strategy A_p which is uninvadable by a rare strategy A_r.

Hitherto in this paper, it has been assumed that a rare strategy meets itself so rarely that the possibility could be ignored in the first instance. When contestants are related, the chance that a strategy meets itself can no longer be ignored; as Grafen (1979) observed, this may change the fine structure of the game in a way not encompassed by naïve inclusive fitness arguments. In the 2-player pool- comaprison game, an individual of quality q playing $A_r(q)$ in a population playing A_p has individual fitness:

$$P(A_p, A_r(q), q) = rV(q)F_r(q) + (1-r)V(q)F(A_p^{-1}(A_r(q))) - C(A_r(q), q) \quad (7.2)$$

where $F_r(q)$ is the cumulative distribution of individuals playing A_r which signal lower than $A_r(q)$. That is:

$$F_r(q) = \int_{A(p)<A(q)} f(p) \cdot dp$$

provided $A_r^{-1}(a)$ has measure zero for all $a \in \mathcal{A}$ (i e. A_r has no horizontal sections). Equation (7.2) is the equivalent of equation (5) of Grafen (1979).

To recapitulate, by assuming that the players are related, the assumption of random choice of opponents from the entire population is destroyed (although it is implicit in equation (7.2) that the distribution of individual qualities is independent of relationship; removing this assumption complicates matters greatly). This assumption was implicit in assuming only a first order structure in chapter 2. Thus, equation (7.2) must split N into two terms: the first term representing the situation in which the strategy has to play against itself, and the second term representing the situation in which the strategy must play against the population strategy.

In these circumstances, the best way of avoiding an erroneous inclusive fitness argument is to take a 'gene's eye' perspective, and calculate the expected individual fitness of strategy that is rare in the population as a whole, but for which a proportion r of its competitors also play the same 'rare' strategy. (From a genetic model perspective, implicit in this is either a haploid model or a diploid model with the rare strategy being dominant). A population strategy A_p is then an ESS if:

$$\int_Q P(A_p, A_p(q), q) f(q) \cdot dq > \int_Q P(A_p, A_r(q), q) f(q) \cdot dq$$

for all strategies that A_r that differ from A_p on a set of measure greater than zero.

If we restrict the allowable strategies to those that are strictly increasing in q, then the term $rV(q)F_r(q)$ is independent of the strategy played (being equal to $rV(q)F(q)$). Thus, the fitness of a rare strictly increasing strategy relative to a strictly increasing population strategy is unaffected by competition between related individuals, and the ESS condition is:

$$\int_Q ((1-r)V(q)F(q) - C(A_p(q), q)) f(q) \cdot dq > \int_Q ((1-r)V(q)F(A_p^{-1}(A_r(q))) - C(A_r(q), q)) f(q) \cdot dq$$

for all strictly increasing A_r that differ from A_p. Repeating the arguments of section 2.2 we see that there exists a unique ESS given by:

$$\frac{dA^*}{dq} = \frac{(1-r)V(q)f(q)}{C_1(A^*(q), q)} \tag{7.3}$$

with initial condition $A^*(q_{\min}) = a_{\min}$.

If $V(q)$ is increasing in q, then:

$$\int_Q rV(q)F_r(q)f(q) \cdot dq \tag{7.4}$$

is maximized when $F_r = F$. That is, from a gene's eye perspective, the optimum strategy for competing in the proportion of contests that are against individuals not bearing the rare strategy gene also coordinates the outcome of the contest in the optimal way in the proportion of competitions that are between individuals both playing the rare strategy (or the equal best way if $V(q)$ is constant on some interval). Thus, if $V(q)$ is increasing, the strategy given by equation (7.3) is an ESS relative to the set of all functions. It may also be shown that when $V(q)$ is strictly increasing, there exists an infinite number of ESSs close to A^*

As r approaches 1, $A'(q)$ becomes extremely small, which in turn implies that $C(A(q), q) - C(a_{\min}, q)$ becomes extremely small. This confirms the intuition that evolutionarily stable, honest, cost-free signals should be able to exist between clones, as cheating your clone is the same as cheating yourself.

On the other hand, setting $r = 0$ in equation (7.3), that is assuming that individuals are unrelated, gives the original result of Proposition 2.1.

A few caveats should be observed here. First, this does not imply that clones should divide resources equally (see previous paragraph). Second, it does not imply that signals between clones should actually be totally free, just that there should be no strategic cost. Costs may be induced in producing signals that are strong enough to be noticed from the background 'noise', and in the case where quality or need is being signalled to a clone, costs may be induced in making the message distinguishable from the messages produced by clones of different qualities or needs. Finally, the above analysis relies upon each of the signallers having the same expected relationship with all the other signallers, as might be the case in a brood of chicks. The above analysis fails when there is an asymmetry in perspective between 'clones' For example, cancer cells in one part of the body could subvert an almost free signalling system because although they are 'not related' to the cells that they are signalling to, the receiving cells have a very high coefficient of relatedness to the population of cells that signal them. In fact, the entire analysis in this paper is based on the assumption that all signallers have the same basic 'beliefs' about the world. Hammerstein & Parker (1982) have analysed the WOA in circumstances in which this may not be true. Initial calculations suggest that a similar analysis can be performed for the kinds of models contained in this paper, however, this would require a substantial extension of the basic analysis in chapter 2.

7.4.2 Coordination Problems

If $V(q)$ is not increasing, then a coordination problem arises when we extend the set of possible 'rare' strategies to include functions that are not increasing. For example, suppose that $V(q)$ is strictly decreasing in q. In this circumstance there are two opposing forces on a rare strategy in the population. On one hand the term:

$$\int_Q rV(q)F_r(q)f(q) \cdot dq$$

is maximized when $F_r = 1 - F(q)$, that is when $A_r(q)$ is a decreasing function of q, whilst the arguments of section 2.2 show that this cannot be an optimal strategy when the competition is against an unrelated individual. In particular, it is easy to check that for any given strictly decreasing $V(q)$ the strictly decreasing strategy:

$$A_r(q) = a_{\min} + \epsilon \frac{q_{\max} - q}{q_{\max} - q_{\min}}$$

can invade any increasing strategy, provided ϵ is small enough and r is large enough. Thus, if $V(q)$ is strictly decreasing and r is large enough, there may not be an increasing ESS to the signalling game.

In summary, if $V(q)$ is strictly decreasing, high quality individuals want to signal at a high level if their competitors are definitely not related to them (as in the results of chapter 2 dealing with competition between unrelated individuals), whilst they want to signal at a very low level if their competitors are actually related to them. This 'desire' to 'throw' the contest if the other competitors are actually related may destabilize the usual handicap signalling equilibrium.

7.4.3 (n+1)-Player Pool-Comparison Games Between Relatives

The argument for two player games is easily extended to pool-comparison between $n+1$ individuals. Equation (7.2) becomes:

$$P(A_p, A_r(q), q) = V[rF(q) + (1-r)F(A_p^{-1}(A_r(q)))]^n - C(A_r(q), q) \quad (7.5)$$

Although the game cannot be simply divided into contests between individuals playing the rare strategy and contests in which the rare strategy plays against the population strategy, similar arguments apply. Provided $V(q)$ is increasing in q, the equation (7.5) can be differentiated to give the first order condition for the ESS:

$$\frac{dA^*}{dq} = \frac{(1-r)nVF^{n-1}(q)f(q)}{C_1(A^*(q), q)} \quad (7.6)$$

By similar reasoning to section 2.2 the unique ESS is the solution to equation (7.6) with initial condition $A^*(q_{\min}) = a_{\min}$.

7.4.4 An Inchoate General Argument

Given equations (7.3) and (7.6), one would like to conclude that, in general, the differential equation defining the ESS for a game between individuals with expected relationship r should be the same as equation (2.8) except for a factor of $1-r$. The problem arises in deriving this result. Equation (7.5) shows that the fine structure of the model cannot be ignored when deriving the payoff function.

One of the fundamental motivations of the treatment given in this paper was to derive results independent of the exact details of the mechanisms involved. Does interaction between relatives make this aim unobtainable?

The answer is that although it does not seem possible to calculate the fitness of an individual playing a rare strategy in a game against relatives, the first order condition for an ESS may be derived by a simple argument when $V(q)$ is increasing.

Suppose that $V(q)$ is constant, and suppose that $A_r(q) = A_p(q)$ except for some q' at which $A_r(q') = A_p(q') + \delta a$, where δa is a small quantity. The fitness of an individual of quality q' playing the rare strategy, A_r, is then increased (to first order) by:

$$VN_2(A_p, A_p(q'))\delta a - C_2(A_p, A_p(q'), q')\delta a$$

From a 'gene's eye' perspective, the marginal increase in cost, $C_2(A_p, A_p(q'), q')$, is certainly paid by the strategy A_r. However, not all of the marginal benefit is accrued by the rare strategy. Although the individual gains fitness at a marginal rate $VN_2(A_p, A_p(q'))$, a portion r of this will, on average, be benefit that the signaller 'stole' from another individual playing the rare strategy A_r. Thus, as $V(q)$ is constant in q, we can conclude that the actual marginal gain to the rare strategy is $(1-r)VN_2(A_p, A_p(q'))$.

If A_r differs from A_p on a set of measure greater than zero, the argument must be extended slightly. As this requires a significant mathematical diversion, it is not set out here.

8 Concluding Remarks on Strategic Signals

8.1 Extension to Sexual Selection and Life Histories in General

Although the models and results in the previous chapters were developed to represent and obtain insight into signalling competitions, their generality allows their application to a much wider class of biological circumstances. This follows from the observation that signalling, as represented in this paper, is merely a special case of the notion of a trade-off. The dual notions of trade-off and constraint are fundamental to life history theory (see Roff 1992; Stearns 1992) and behavioural ecology and, thus, we should expect the models presented here to be widely applicable.

The basic situation represented by the models presented in this paper is that of two antagonistic components of fitness: fitness components that are constrained so that increasing one of them results in a decrease of the other. These components are represented by VN and C (or S). The parameter that determines where on the continuum of values that these fitness components may take is a, the level of signal. Although a is assumed to have physical manifestation in this paper, such a parameter could equally represent a more invisible quality, such as the apportionment of resources between the immune system and gamete production.

There are two additional factors included in the formulation of trade-offs presented here, that do not usually appear in treaments of life history theory. The first of these, the inclusion of individual quality, resource base, or habitat quality, q, has been recognised as an important factor when determining the expected intraspecific correlation that should be observed in a wild population between various antagonistic life history traits (Stearns 1992). The second is the ability of the models to cope with feedback between the population strategy and the optimal individual strategy. Quality has not usually been an explicit part of life history models: if there is no feed back then the effects on observations of variation in indviduals' quality can be treated by simply looking at the equilibrium values of the model for different initial resources. However, the rejection of group selection as a major force in evolution by most biologists (e.g. Williams 1966 or Dawkins 1976; though see Wynne-Edwards 1962, 1986 and Wilson 1989 for an opposing viewpoint) highlights the observation that more often than not an individual's most strident competitors are members of its own species. In these circumstances, surely we must expect feedback between individual and population strategies.

With the observation that strategic signalling models do not differ from many other life history models in form, it becomes quite clear that there is no theoretical justification for distinguishing between 'natural' and 'sexual' selection, as Darwin (1871, Vol 1 p278) and countless others have attempted. In particular, Zahavi's (1987) attempt to shift the demarcation to natural selection versus signal selection, from mechanistic arguments ('signal selection differs from the evolution of all other kinds of trait') is doomed to failure.

This is not a new observation; J.B.S. Haldane (1932) and Julian Huxley (1938a,b, 1942) both pointed out that the logical form of 'sexual selection' did not differ from the form of many other kinds of intraspecific selection and, as shown here (e.g. section 4.4), from some types of interspecific selection. Although there is a tension between many conflicting ideas in Huxley's papers on sexual selection which undeniably led him into assertions that are hard to defend, I would suggest that it is perhaps too easy to dismiss Huxley's (1938a,b) discussions of selection as 'confused' and 'obscured... by a thicket of complicated terminology' as Andersson (1994) has done. Many of the concepts demarcated and named by Huxley are important and show deep insight. Darwin's ideas may be simple and easy to grasp, but I do not believe that they can stand up to anything more than cursory inspection.

II

Epistatic Handicaps

9 A Game Theory Model of the Epistatic Handicap

9.1 A Brief Review

In various reviews, Maynard-Smith (1985, 1987, 1991; see also Møller 1994) has proposed that there are at least three conceptually distinct mechanisms by which handicaps *sensu* Zahavi (1975, 1977) might evolve. Two of these mechanisms, the revealing and conditional (or strategic) handicaps, have overcome initial theoretical skepsis (Davis & O'Donald 1976; Maynard-Smith 1976, 1978; Bell 1978), by finding support in mathematical models (Grafen 1990a; Iwasa et al. 1991). However, the third mechanism, known as the epistatic or Zahavian handicap mechanism, has not found such support (Maynard-Smith 1991; Collins 1993). In fact, it has been considered so unsuccessful that it was disregarded in a recent review of the empirical evidence for handicaps (Johnstone 1995).

A handicap is said to be purely epistatic if there is no direct relationship between the quality signalled and the level of expression of the handicap trait prior to the effects of natural selection (i.e. the effects on survival of the handicap). This is to be contrasted with revealing and conditional handicaps in which the expression of the trait is quality dependent.

In this paper, it is shown that the epistatic handicap mechanism is not unreasonable from a theoretical perspective, and thus any rejection of this mechanism can only come from an empirical source. To this aim, three distinct models of the mechanism are provided: a continuous game theory model, a quantitative genetics model, and a three locus major gene model.

The continuous game theory model is important for a number of reasons over and above the fact that it exhibits the epistatic handicap mechanism functioning successfully. First, it clearly delineates sufficient conditions for the mechanism to work in the absence of any other sexual selection mechanism. Second, the model is constructed in a way which allows direct comparison with the very successful strategic handicap model of Grafen (1990a). This comparison highlights important distinctions between the epistatic and strategic handicap mechanisms, as well as showing how the two are related. In this way, it improves our understanding of both.

The quantitative genetics and three locus models also have implications over and above supporting the viability of the epistatic handicap process. In particular, they are used to show that an argument about genetic correlations at equilibrium that has appeared repeatedly in the literature is specious. The rejection of this argument leads to the reversal of one published conclusion, and the modification of others.

9.2 Negating the Fisher Process

Many early analyses of the handicap principle eliminated the possibility that evolutionarily stable strategies (ESSs) that were obtained were due to the Fisher process (O'Donald 1980; Lande 1981; Kirkpatrick 1982; Pomiankowski et al. 1991 for models of the Fisher process) by assuming that the mating system was strictly monogamous. With this assumption, the epistatic handicap mechanism appeared to work only in the most extreme circumstances (see Andersson 1994 for review).

However, this is not the only way in which Fisherian effects can be removed from models of sexual selection. The Fisher process requires there to be additive genetic variance in the male trait that females are favouring, because the female preference only spreads indirectly, by the induced correlation between the selected trait genes and the preference genes. One way to remove this effect is to artificially destroy the correlation in the model at each generation, an approach taken by Maynard- Smith (1976).

Another way to avoid the correlation by which the Fisher process operates is to assume that there is no additive genetic variance in the male trait whilst a gene for female discrimination is attempting to invade. If this is the case and female preference still spreads, then we can conclude that this effect is not due to the Fisher process. (It should be stressed here that, although I refer to active female selection of males by words such as 'discrimination', 'choosiness' and 'preference', all the arguments contained in this paper apply equally to passive female selection.) Similarly, if female discrimination is costly and only the Fisher process is operating, at an ESS in which females are discriminating there must be additive genetic variance in the male trait, for if there was no variance there could be no advantage from being discriminating to outweigh the cost. These observations are used in the following model of the epistatic handicap process. They have been used previously in the context of strategic handicaps by Grafen (1990a).

9.3 Basic Description of Model

The following model of sexual selection is dissimilar in style to all previous models of sexual selection, though it is most similar to recent strategic handicap models (Grafen 1990a,b; and chapters 2 to 7). The parameters in the model are continuous and it may be considered solely as equilibrium analysis, outlining only which pairs of male and female strategies are evolutionarily stable, and not how these strategies may be reached. However, the analysis can be extended by the addition of a second concept which accommodates the genetic concern: is it possible to reach a particular equilibrium from some predetermined state? For instance, whether it is possible to reach an equilibrium in which males bear a handicap trait and females are discriminating, from one in which there is no handicap and no discrimination entirely within the constraints of the model (e.g. some models of sexual selection (Pomiankowski 1988) have needed to assume that a certain threshold of female discrimination needs to be passed before the 'runaway' process begins). This concept of 'reachableness' is defined properly hereinafter.

As the model deals with a handicap mechanism it considers three main characters:

1. A quality of interest to females (either genetic or phenotypic). Females which mate with males of high quality are assumed to have high reproductive success. This quality is denoted by q, and may range over $[q_{\min}, q_{\max}] \stackrel{\text{def}}{=} Q$. The population's quality is continuously distributed with

probability density denoted by $f(q)$. There are no assumptions made about the proportion of this variance in quality that is due to additive genetic variance; all that is assumed is that the distribution of quality is constant over time (before considering the effects of the sexually selected trait), and that females benefit in some way by mating with high quality males. Although this may not be reasonable for a dynamic model, the assumption is valid for the purpose of equilibrium analysis; one assumes, *post facto*, that $f(q)$ is the equilibrium distribution. Effects of dynamic assumptions are considered as they arise.

2. The (potentially) exaggerated trait borne only by the selected sex (henceforth assumed to be the male sex). The trait's phenotype is denoted by the variable a, which may take values in $[a_{\text{min}}, a_{\text{max}}] \overset{\text{def}}{=} \mathcal{A}$. It is assumed that before trait-induced-mortality, the mean male trait magnitude is determined by a single parameter, t, which is called the trait genotype; t is assumed to take on values in $[t_{\text{min}}, t_{\text{max}}] \overset{\text{def}}{=} \mathcal{T}$ A male with genotype t expresses the trait at a level a with probability density $e(a,t)$, where $\bar{e}(a,t) = t$.

   To simplify analysis, it is assumed that the effect of t on ϵ is solely one of translation, i.e. $e(a,t) = e(a-t,0)$. The phenotypic variance, e, is assumed to be due either to environmental effects or genetic interactions, both of which are assumed to be uncorrelated with q. This lack of correlation between the development of the trait and an individual's quality may seem unlikely, but it is what makes an epistatic model 'epistatic' It should be noted that the assumption that the trait is determined by a single parameter does not imply that the trait is determined by a single locus.

3. The intensity of preference of selecting sex (henceforth assumed to be the female sex). To simplify analysis, females are assumed to be phenotypically identical. The actual set of strategies used by females, and the relevant notation, is described below.

The assumption of environmental variance in the trait turns out to be necessary for the particular model to work. This should not be seen as special pleading (the major gene model does not include any environmental variance); if anything, as environmental variance is so ubiquitous, neglecting it should be considered an assumption that needs to be justified.

The model is analyzed in two stages. In the first stage, it is treated purely as an equilibrium analysis, which avoids, among other things, some of the complications that can arise from genetic covariances. The second stage introduces genetics to the model, and shows that its effect is negligible.

9.4 Effect of Trait on Male 'Survival'

Females are assumed to choose mates from a random sample taken from a pool of 'available' males. A given male of quality q bearing a trait of phenotype a is assumed to have probability $S(a,q)$ of being in this pool at any given point in time. In a semelparous species, S might represent the probability that an individual male survives until the breeding season; in an iteroparous species it could represent the life expectancy of an individual. Because of these interpretations

S shall be referred to as the probability of 'survival'. However, S need not be a measure of mortality; it could equally be a measure of the proportion of the breeding season of which an individual is able to attend a lek, or the proportion of the day which may be spent attempting to attract mates.

The cumulative distribution function of 'available' males of genotype t is thus given by:

$$x(a,t) = \frac{1}{\bar{S}(t)} \int_{a_{min}}^{a} \int_{Q} e(b,t)S(b,q)f(q) \cdot dqdb \tag{9.1}$$

where $\bar{S}(t)$ is the normalizing function:

$$\bar{S}(t) = \int_A \int_Q e(a,t)S(a,q)f(q) \cdot dqda$$

The effect of S on the distribution of male quality is crucial to the functioning of the epistatic handicap. Mean 'available' male quality is increasing in the phenotypic trait if:

$$\frac{S_1(a,q_1)}{S(a,q_1)} \leq \frac{S_1(a,q_2)}{S(a,q_2)} \quad \text{whenever } q_1 < q_2 \tag{9.2}$$

for almost all (a,q) for which $S(a,q) \neq 0$. (Note that the notation S_i denotes the partial derivative of S with respect to the ith variable.) More precisely, mean male quality is strictly increasing on regions in which the inequality is strict for all a and q, and is constant on regions in which the inequality is an equality for almost all q. These assertions are proven rigorously in Appendix B (setting $p = a$, $u = S$ and $R(q) = q$), but may be seen intuitively as follows: As the set of infinitely differentiable functions is dense in the set of continuous functions, it is not much of a restriction to assume that S is at least thrice differentiable. In this case, equation (9.2) may be written:

$$\frac{\partial}{\partial a}\left(\frac{S_2(a,q)}{S(a,q)}\right) = \frac{\partial}{\partial q}\left(\frac{S_1(a,q)}{S(a,q)}\right) \geq 0 \quad \text{a.e.} \tag{9.3}$$

wherever $S \neq 0$. The left hand side of the above equation states that the ratio of survival of individuals of a marginally higher quality relative to the survival of individuals of quality q is increasing in the level of the phenotypic trait size.

For females to be strictly better off by selecting males with large trait phenotypes, indirectly obtaining mates of higher quality, the inequality of equation (9.2) must be strict between two sets of males of non-zero expected frequency in the population. (This is discussed further when the specific model of female choice is constructed.) This was stated as a necessary criterion by Zahavi (1975,1977) and the assumption appears in all strategic handicap models. It was also observed in the first model of handicap selection by Maynard-Smith (1976). Grafen's (1990a, p475) condition on survival for his multiplicative strategic handicap model is equivalent to equation (9.2) with strict inequality. Equivalent inequalities appear in other strategic handicap models (Iwasa et al. 1991; Vega-Redondo and Hasson 1993). It should be noted that no assumptions have been made about the signs of S_1 or S_2. Increasing mean male quality requires only that equation (9.2) holds, and this may be true even if survival is positively correlated with trait magnitude, or negatively correlated with quality. However, it would normally be expected that $S_1(a,q) < 0$ and $S_2(a,q) \geq 0$.

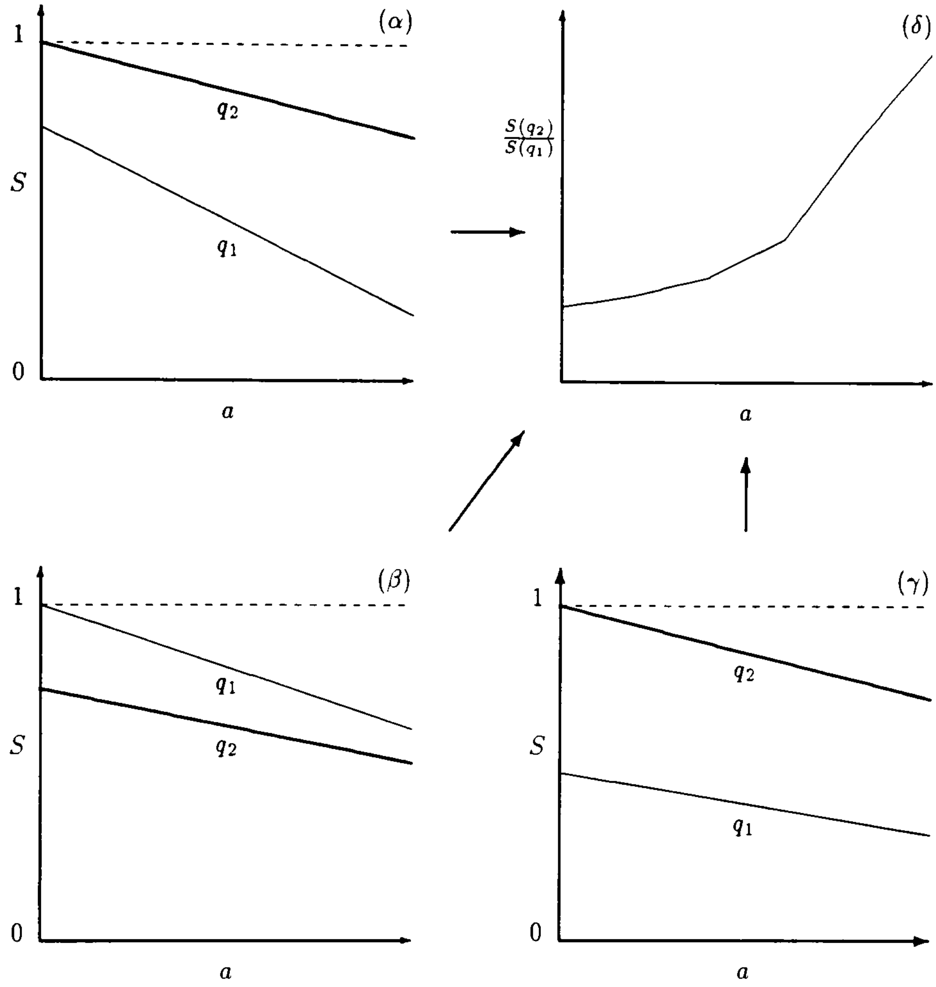

Figure 6: [Graphical illustration of the meaning of equation (9.3)] *Females benefit by choosing males which bear a large trait because of the increasing difference in the ratio of high and low quality males (q_2 and q_1 respectively) that survive bearing the handicap, as illustrated in graph (δ). Possible survival functions, S, for low and high quality males are given in graphs (α), (β), and (γ) all of which give rise to expected male quality being increasing in a. Graph (α) represents an intuitive form of $S(a, q)$ which satisfies equation (9.3), in which high quality males have higher absolute survival and lower absolute marginal survival costs of bearing large handicap trait than low quality males. Neither of these conditions are necessary for equation (9.3) to be satisfied. Graph (β) illustrates an $S(a, q)$ which satisfies equation (9.3) but for which high quality males have lower absolute survival than low quality males. Graph (γ) illustrates an $S(a, q)$ which satisfies equation (9.3) but for which high quality males suffer higher marginal survival costs of bearing larger handicaps than low quality males. If equality held in equation (9.3) for all q between q_1 and q_2 for all a, then the graph (δ) would be flat.*

The case in which $S_2(a, q) < 0$ for all a highlights an important distinction between absolute and relative mating success. Active female preference for males that bear large ornaments requires the relative chance of a male being high quality to be increasing in the size of trait that he bears. This does not imply that the actual chance that a male survives to the breeding season needs to be positively correlated with his quality (see Fig.6). Thus, it is perfectly possible for males of high quality to have lower survival than low quality males, which implies that it is possible for reproductive success to be negatively correlated with the quality of males prior to the effects of survival selection on the male population, though with active female discrimination, the correlation between male quality after survival selection and reproductive success must be positive. With passive female mate selection, however, even this need not be the case (Siller 1997).

In contrast to handicap traits, a trait is purely aesthetic or 'Fisherian' if there is no interaction between the trait's effect and the effect of an individual's quality on the individual's survival. That is, $S(a, q)$ is a separable function:

$$S(a, q) = \hat{S}(a)\check{S}(q) \tag{9.4}$$

Note, that if S satisfies equation (9.4) then it satisfies equation (9.2) with the inequality sign replaced by an equality sign. If S satisfies equation (9.4) then, for all a, the expected quality of males is independent of the phenotypic level of trait borne. In this circumstance, a female who selects a male bearing a large trait gains nothing in terms of increased expected quality of mate. If this condition is assumed this model becomes equivalent to Parker's (1983) formulation of the Opponent Independent Costs Game.

It should be noted that these conditions on quality dependent survival are only important when female preference is active. When female choice is passive (e.g. they move up sound gradients), or the main benefits of the male trait to females is to facilitate their finding males to mate with, then effective female selection for exaggerated male traits may be supported without quality dependence.

9.5 Female Strategy

Choosing the individual with the largest trait from the set of males sampled is the best (or equal best) strategy if whenever the fitness of a female, R, is an increasing function of the quality of her mate then the expected reproductive success of a female:

$$E(R, a, t) = \int_Q R(q, t) \frac{S(a, q) f(q, t)}{\int_Q S(a, q) f(q, t) \cdot dq} \cdot dq \tag{9.5}$$

is an increasing function of the phenotypic trait magnitude of her mate. This follows from equation (9.2) and Appendix B. Furthermore, $E(R, a, t)$ is strictly increasing in a between regions in which the inequality in equation (9.2) is strict for almost all q and is constant between regions in which the inequality is an equality for almost all q. Note that the variable t in R represents the population genotype, not the individual genotype.

Equation (9.5) is only correct when the vast proportion of the population have the same trait genotype. When more than one trait allele has substantial frequency in the population, Fisherian effects need to be considered. For a given population distribution of males, the net result of there being more than one trait genotype in the population would be to increase the expected fitness to be gained by mating with males with a large trait and to decrease the expected fitness benefit of mating with a male bearing a small trait. However, this effect only increases the intensity of selection for females to be discriminating. This effect is disregarded in what follows, because it is hard to quantify without introducing genetics explicitly, and disregarding it only makes it more difficult for the epistatic handicap mechanism to work. Similarly, if the quality that is being selected for is genetic, then correlations between quality and the trait, and quality and female preference, will be positive. Assuming that there is no correlation between quality and the other traits also retards the epistatic mechanism.

For ease of analysis, it is assumed that females choose the male who bears the largest trait of n males randomly sampled from the pool of available males: the 'best of n' strategy (Seger 1985). This is also known as the pool-comparison strategy (Janetos 1980, Real 1990), or partial mating preference (O'Donald 1980). Unless the inequality in equation (9.2) is strict for almost all pairs of qualities, this strategy is only the equal best strategy for females selecting from samples of n, as there is no difference in expected qualities of individuals on connected regions $\mathcal{A}_i \in \mathcal{A}$ for which equality holds in equation (9.2) for all $a \in \mathcal{A}_i$; in this situation females need not discriminate between individuals within the regions $\mathcal{A}_i$.

The cost of choosing from n individuals is given by $C(n,t)$ and the expected fitness of a female choosing from a sample of n males mating with a male with phenotypic trait a is then $E(R,a,t) - C(n,t)$.

The additivity of this definition of fitness is potentially problematic. For example, what would be meant by $E - C$ taking on a negative value? The best way around this problem is to view $E - C$ as logarithmic fitness, where actual 'fitness' is the exponential of $E - C$. From this perspective, negative fitness is not a negative number of offspring, but a fitness of less than unity which, assuming the correct choice of units, may be interpreted as the female expecting to provide less than one copy of here genes to the next generation. The additive partition of female fitness has been used here, as it simplifies a number of calculations performed later.

Note that by a previous discussion, $E - C$ may not be a measure of fitness, *per se*, but a measure of fitness relative to other females of the same quality, e.g. $E - C$ might be viewed as the fitness per zygote produced. So actual female fitness might best be viewed as a function of the form:

$$Z(q_f)\exp(E)\exp(-C) \quad \bullet$$

where q_f is the female's quality, Z the maximum number of zygotes she can expect to produce if she were to live to her maximum life span, the exponential of E the expected quality of these zygotes, and the exponential of C the proportion of her maximum lifespan that she can expect to live. Taking logarithms shows that the female strategy will be independent of Z in this particular example.

If all the males in the population are of genotype t, the distribution function of level of trait displayed by the males chosen by females choosing from n is given by $nx^{n-1}(a,t)x_1(a,t)$. This is easily derived for integer n. However, as it will be useful to assume a continuum of levels of female choosiness, the obvious continuous extension to non-integer n is assumed. This makes sense if n is viewed, not as the actual number of males sampled, but as an abstract representation of the intensity of female discrimination. Note that $n = 1$ represents the situation in which females mate randomly, and $0 < n < 1$ the situation in which females favour males with smaller phenotypic traits. It will be assumed in the following that $n \geq 1$.

The following result was proven in section 5.1.

Proposition 9.1 *Assume that* $C_1(n,t) > 0$ *and* $C_{11}(n,t) > 0$, *that is both the cost of choice and the marginal cost of choice are increasing in* n, *and that* $C(n,t)$ *is continuous in* t. *Further assume that* $E(R,a,t)$ *is increasing. If all the males in the population are of genotype* t, *then there exists a unique optimal intensity of female discrimination,* $N(t)$. *Moreover, for all* t *for which* $\bar{S}(t) \neq 0$, $N(t)$ *is continuous.*

Denote by $P(n,t)$ the expected fitness of a female playing the strategy 'choose the best of n', due to the expected quality of her mate given that all males in the population are of trait genotype t (recall that this assumption negates Fisherian effects):

$$P(n,t) = \int_{\mathcal{A}} E(R,a,t) n x^{n-1}(a,t) x_1(a,t) \cdot da$$

Observe that if $P_1(1,t_{\min}) - C_1(1,t_{\min}) > 0$, then, regardless of whether the male trait evolves away from its natural selection optimum, $t_{\min}$, 'slightly' discriminating females will have higher fitness than females which mate randomly.

This highlights the basic distinction between the Fisher process and the epistatic handicap mechanism. If t is a purely Fisherian trait, $E(R,a,t)$ is independent of a, which implies, by Appendix B, that $P_1(n,t) = 0$ for all n and t. In other words, if the effects of discrimination on female fitness are due solely to more discriminating females choosing males who will produce more attractive sons, and all the fathers carry the same trait genotype whose expression is quality independent, then there can be no benefit in discriminating and, thus, costly discrimination behaviour will be selected against. If discrimination is costly to females, there cannot be an ESS at which females discriminate between males and the male population has only one trait genotype, unless some information about a quality of interest to the females can be inferred from the phenotypic expression of the trait.

From a more mechanistic perspective, in models of the Fisher process, female preference for males bearing large traits spread only because there is an induced correlation between preference and trait genotype. If there is no additive genetic variance in the male trait, the preference cannot spread. Further, costly female choice can only be supported if there is additive genetic variance in the male trait at equilibrium. Epistatic handicaps allow female discrimination to spread when there is no variance in the male trait genotype as females gain fitness by the correlation between the phenotypic male trait and quality.

In terms of the model, if the trait in question is a purely Fisherian trait then the only pure ESS to the model is females not discriminating and the population male genotype being at the natural selection optimum. Thus, if an ESS, other than the trivial one, exists to the model outlined here it can be attributed solely to the epistatic handicap mechanism. Such an ESS is given in Example 2 below.

9.6 Does this Model Encompass Selection for 'Good Genes'?

Previously it has been stated that there has been no assumptions made about the proportion of the variance in q that is due to additive genetic variance in male quality. Equivalently, there have been no assumptions made about whether the benefits received by females choosing males of high quality are direct benefits or due to 'good genes'. How can $R(q,t)$ take into account 'good genes' without explicit genetic modelling? First, it must be noted that, as the following is primarily an analysis of equilibria that are genetically monomorphic in female discrimination strategy and mean male trait, we need not be concerned about genetic correlations between the discrimination, male trait, and quality loci. By the assumption that females are identical in their relative costs and benefits of discriminating between males, at an equilibrium that is monomorphic in male trait and female discrimination, there is no correlation between a females 'quality' and the quality of the male that fathers her offspring. Thus, on average, a female which happens to mate with a male of higher quality than the average quality of mates chosen by other females in the population will have higher quality daughters, and higher quality sons than expected. The benefit of having high quality sons is obvious from the model, provided that $S_2(a,q) \geq 0$; if a female has a high quality son then he is more likely to survive relative to a low quality son that developed the same level of handicap trait. Explicit calculations are required to verify that active female discrimination can be supported if $S_2 < 0$, as in some circumstances this may not be the case. The benefit of having high quality daughters is not explicit in the model because relative discrimination costs have been assumed to be the same for all females, as might be the case if C was a logarithmic measure of surviving the process of discriminating between males. However, the benefit of having high quality daughters can be dealt with implicitly by $R(q,t)$ being increasing in q.

Another requirement of a 'good genes' model of sexual selection, that is not made explicit in the model given here, is the process by which additive genetic variance in quality is maintained in the population. Again, no assumptions have been made about this. There are numerous mechanisms extant in the literature that can maintain additive genetic variance in a population such as mutation (e.g. Charlesworth 1987, Rice 1988), parasite coevolution (Hamilton & Zuk 1982), and more general spatio-temporal heterogeneity of environments coupled with migration or dispersal of offspring (Bell 1982). As mentioned previously, for ease of analysis, $f(q,t)$ is assumed to be an equilibrium distribution of male quality.

Finally, if male quality is heritable, intensity of female choice should affect the functions R and f. For example, more intense female discrimination should lower the variance of f. This has not been assumed as it makes the analysis of the model slightly more cumbersome, but does not change the central results. How to solve the model under the assumption that R and f are functions of n is indiciated by the following result:

Proposition 9.2 *Assume the conditions of Proposition 9.1, with the added assumptions that $R(q,n,t)$ and $f(q,n,t)$ are continuous in n with respect to the integral norm over q, and that $R(q_{\max},n,t)$ is bounded in n for each t. Then for each t there exists at least one optimal intensity of female discrimination.*

Proof: Define $G(n,t)$ to be $N(t)$ as calculated in the proof of Proposition 1 for $E(R,x) = E(R,x,n)$. Thus $G(n,t)$ is unique for each (n,t). As $C_{11}(n,t) > 0$ and $E(R,x)$ is bounded above by the assumption on $R(q_{\max}, n, t)$, then for each t there exists a $n_{\max}(t)$, so that $G(n,t)$ is contained in $[0, n_{\max}]$ for all $n \in [0, \infty)$. Clearly, any fixed point of G is an optimal female response. By equation (9.5), $E(R,a)$ is continuous in n. This implies, by equation (9.1), that $E(R,x,n)$ is continuous in n, and thus $G(n,t)$ is continuous in n (This is intuitively obvious, but may be proven rigorously by Lemma 2.8. By Brouwer's Fixed Point Theorem (Rotman 1988), there exists at least one fixed point of G, and thus, for each t, there exists at least one optimal female response. □

9.7 Male Fitness

Consider a population in which almost all males are of trait genotype t_p and females play strategy n. The expected relative fitness of a rare male of genotype t in such a population is:

$$M(n,t,t_p) = \frac{\bar{S}(t)}{\bar{S}(t_p)} \times \frac{n}{\bar{S}(t)} \int_A \int_Q E(R,a)e(a,t)x^{n-1}(a,t_p)S(a,q)f(q) \cdot dqda$$

The term on the left side of the multiplication sign represents the relative survival of the genotype, which is strictly decreasing in t. The right hand term represents the relative success in competition for matings of an individual of genotype t, when t is rare (i.e. ignoring second order terms).

Substituting the equation for $E(R,b)$, this may be written:

$$M(n,t,t_p) = \frac{n}{\bar{S}(t_p)} \int_A \int_Q R(q)e(a,t)x^{n-1}(a,t_p)S(a,q)f(q) \cdot dqda$$

The problem is to find a pair of male and female strategies/genotypes which are an ESS. Unfortunately, this is not possible to do in general. The following examples, however, show that the male trait being at its natural selection optimum and females not discriminating may not be an ESS (Example 1), and that non-trivial ESSs do exist, and may be reached from an initial condition of females not being discriminating (Example 2).

It will prove useful to adopt the notation (n,t) to represent a population in which females choose from n males and males carry trait genotype t.

Example 1: The following example shows that $(n,t) = (1, t_{\min})$ need not be an ESS. Let $e(a,t)$ be a normal distribution with standard deviation σ. The derivative of the male payoff, $M(n,t,t_p)$ with respect to t is then:

$$M_2(n,t,t_p) = \frac{n}{\bar{S}(t_p)} \int_A \int_Q \frac{1}{\sqrt{2\pi\sigma^3}} R(q,t)(a-t)\exp\left(\frac{-(a-t)^2}{2\sigma^2}\right) x^{n-1}(a,t_p)S(a,q)f(q) \cdot dqda$$

It is easy to see that the integral for $M_2(1,t,t_p)$ is symmetric in a around t except for the function $S(a,q)$ which is (by assumption) decreasing. Therefore $M_2(1,t,t_p) < 0$ and the best response to any t_p is $t = t_{\min}$, which in turn implies that if the intensity of female discrimination is low the only possible male ESS is the genotype $t_{\min}$.

However, if n is great enough then $M_2(n, t, t_{\min}) > 0$ and thus $t_p = t_{\min}$ is not an ESS. This follows from the observation that:

$$\lim_{n\to\infty} \left(\frac{x(t_{\min} - a, t_{\min})}{x(t_{\min} + a, t_{\min})}\right)^n = 0$$

provided $a \neq t_{\min}$. Thus, if the best female response to $t_p = t_{\min}$ is large enough, there will be selection for increasing trait size in males. If S and σ are fixed, the optimum level of discrimination is dependent only upon K. It is easy to see that a K can be constructed so that $N(t_{\min})$ will be such that $(N(t_{\min}), t_{\min})$ is not an ESS (e.g. if n is 'large enough' set $K_{11}(m, t_{\min}) = 1/2n$ and $K_1 = (1 + \frac{m-n}{2n})P_1(n, t_{\min}))$.

For general $S(a, q)$ satisfying equation (9.2) it is not true that for every $\epsilon(a, t)$ there exists a level of female discrimination, n, so that $(n, t_{\min})$ is invadable by some other male trait genotype; a pathological situation which illustrates this is discussed in Example 2.

9.8 Genetics

Before proceeding with the second example, it will be useful to make some observations about genetics, and to define the concept of 'reachableness' mentioned earlier (cf. section 2.2.10). First, recall that the analysis looks for equilibria that are homogenous in both female discrimination and the male trait as in this case costly female discrimination and exaggerated male traits cannot be supported by the Fisher mechanism. Further recall that out of equilibrium, it is assumed that there is no correlation between quality, preference, and trait genotypes. This is an artificial assumption, unless variance in quality has no component of additive genetic variance, and female discrimination and the male trait genotypes are not heterogenous in the population at the same time. However, ignoring the expected correlations just makes it more difficult for the epistatic handicap to work.

The fitness of female discrimination genotypes are independent of each other. Therefore, if a rare genotype, n_1, is fitter than n_2 in a population, it will always be fitter in that population, assuming that the distribution of male trait genotypes does not change. Thus, if a female discrimination trait can invade, the invasion will go to completion.

The fitness of male trait genotypes, on the other hand, is relative. Consequently, a trait allele being able to invade does not guarantee that the invasion will go to completion. A male trait allele t_2 will be said to be able to replace a male trait allele t_1 if in a population consisting of both alleles t_2 is always fitter than t_1 regardless of their relative representation.

The notation $(n_1, t_1) \prec (n_2, t_2)$ represents the situation in which either:

1. t_2 can replace $t_1$in a population of genotype (n_1, t_1) and n_2 can invade a population of genotype (n_1, t_2); or
2. n_2 can invade in a population of genotype (n_1, t_1) and t_2 can replace t_1 in a population of genotype (n_2, t_1).

For notational convenience it is assumed that an allele can replace itself. Note that the relationship $\prec$ is not necessarily transitive.

A genotype (n, t) will be said to be reachable from (n_0, t_0) if there exists a finite sequence of trait alleles t_i $(0 \leq i \leq n)$ such that:

$$\begin{array}{rcl} (n_0, t_0) & \prec & (N(t_0), t_0) \\ (N(t_i), t_i) & \prec & (N(t_{i+1}), t_{i+1}) \\ (N(t_n), t_n) & \prec & (n, t) \end{array}$$

Example 2: Assume $e(a, t)$ is given by:

$$e(a,t) = \begin{cases} 1 & \text{if } a \in [t - \frac{1}{2}, t + \frac{1}{2}] \\ 0 & \text{otherwise} \end{cases}$$

Then:

$$M(n, t, t_p) = \frac{n}{\bar{S}(t_p)} \int_{t-\frac{1}{2}}^{t+\frac{1}{2}} \int_Q R(q) x^{n-1}(a, t_p) S(a, q) f(q) \cdot dq da.$$

and

$$\begin{array}{rcl} M_2(n,t,t) & = & \frac{n}{\bar{S}(t)} \int_Q R(q) S(t + \frac{1}{2}, q) f(q) \cdot dq, \qquad \text{if } n > 1 \\ M_2(1,t,t) & < & 0 \end{array}$$

as $x(t - \frac{1}{2}, t) = 0$ and $x(t + \frac{1}{2}, t) = 1$. Thus, noting that M_1 is continuous in the second and third variables, as long as $N(t) > 1$ and $S(t + \frac{1}{2}, q_{\max}) \neq 0$, t is not an ESS, as strategies whose mean trait expression is slightly higher than t can invade.

The fitness of an individual male is dependent upon his phenotypic trait and is independent of his trait genotype. Thus, as $e(a, t)$ is flat, the difference in fitness between two trait genotypes is determined solely by the difference in fitness of trait phenotypes that only occur for one of the trait genotypes. Set $\mathcal{A}_i = [t_i - \frac{1}{2}, t_i + \frac{1}{2}]$ and $\mathcal{A}_{ij} \stackrel{def}{=} \mathcal{A}_i \cup \mathcal{A}_j - \mathcal{A}_i \cap \mathcal{A}_j$. If i is distinct from j then $\mathcal{A}_{ij}$ has two distinct components of equal size. Denote these by $\mathcal{A}_{ij}^-$ and $\mathcal{A}_{ij}^+$ where $\mathcal{A}_{ij}^+$ is the component containing the largest real numbers. If $t_i < t_j$ then only individuals of genotype t_i can have phenotypes in $\mathcal{A}_{ij}^-$ and only individuals of genotype t_j can have phenotypes in $\mathcal{A}_{ij}^+$.

First suppose that $S(t_1 + \frac{1}{2}, q_{\max}) \neq 0$, then t_2 can only invade t_1 if $t_2 > t_1$ because if $t_2 < t_1$ at infinitesimally low frequencies the fitness of individuals of phenotypes $\mathcal{A}_{12}^-$ is zero, whilst individuals of phenotype $\mathcal{A}_{12}^+$ is positive. Moreover, by the equation for M_2 there exists a t_2 for each $n > 1$ which can invade (n, t_1). If t_2 can invade (n, t_1) then:

$$\frac{\int_{\mathcal{A}_{12}^+} \int_Q R(q) S(a, q) f(q) \cdot dq da}{\int_{\mathcal{A}_{12}^+} \int_Q R(q) x^{n-1}(a, t_1) S(a, q) f(q) \cdot dq da} > 1 \qquad (9.6)$$

The left hand side of equation (9.6) is the ratio of the summed fitness of individuals of trait genotype t_2 which are of a phenotype that cannot be expressed by an individual of trait genotype t_1, over the summed fitness of individuals of trait genotype t_1 which are of a phenotype that cannot be expressed by an individual of trait genotype t_2. Note that x has been dropped from the numerator as $x(a, t_1) = 1$ on $\mathcal{A}_{12}^+$.

Assume that $t_2 > t_1$. The relative fitness of genotype t_2 in a population consisting of a proportion p of individuals of genotype t_1 and $1 - p$ of genotype t_2 is then:

$$\frac{\int_{\mathcal{A}_{12}^+}\int_Q R(q)(p + (1-p)x(a,t_2))^{n-1}S(a,q)f(q) \cdot dqda}{\int_{\mathcal{A}_{12}^+}\int_Q R(q)p^{n-1}x^{n-1}(a,t_1)S(a,q)f(q) \cdot dqda}$$
$$> \frac{\int_{\mathcal{A}_{12}^+}\int_Q p^{n-1}R(q)S(a,q)f(q) \cdot dqda}{\int_{\mathcal{A}_{12}^+}\int_Q R(q)p^{n-1}x^{n-1}(a,t_1)S(a,q)f(q) \cdot dqda} > 1$$

where the last inequality comes from equation (9.6). Thus if t_2 can invade (n, t_1), then it can replace t_1.

A similar argument shows that if $S(t_1 + \frac{1}{2} - \epsilon, q_{\mathrm{max}}) = 0$ for some $\epsilon > 0$ then for all n there exists a trait genotype $t_2 < t_1$ which can replace t_1 in (n, t_1). Thus, if $n > 1$ then (n, t) can be an ESS only if $S(t_1 + \frac{1}{2}, q_{\mathrm{max}}) = 0$ and $S(t_1 + \frac{1}{2} - \epsilon, q_{\mathrm{max}}) > 0$ for all $\epsilon > 0$ or if $t = t_{\mathrm{max}}$.

From a pure game theory perspective, it may be concluded that $(N(t), t)$ is an ESS if and only if t satisfies the conditions of the previous paragraph and $N(t) > 1$.

If we include the genetic assumptions, then there are three cases:

1. If $N(t_{\mathrm{min}}) = 1$ then no discriminating female genotype may invade the population. In this case, the only ESS reachable from $(1, t_{\mathrm{min}})$ is itself.

2. Let $\mathcal{T}_+ \overset{\mathrm{def}}{=} \{t; S(t + \frac{1}{2}, q_{\mathrm{max}}) > 0\}$ and denote its closure by $\overline{\mathcal{T}_+}$. If $N(t) > 1$ for all $t \in \overline{\mathcal{T}_+}$ then the only ESS reachable from $(1, t_{\mathrm{min}})$ is $(N(\sup \mathcal{T}_+), \sup \mathcal{T}_+)$. If $t_{\mathrm{max}} = \infty$ and $\mathcal{T} - \mathcal{T}_+ = \emptyset$ then there is no ESS. Note that for a given S it is always possible to choose a $K(n, t)$ so that $N(t) > 1$ for all $t \in \overline{\mathcal{T}_+}$ using the construction given in Example 1.

3. If $N(t)$ is not greater than 1 for all $t \in \overline{\mathcal{T}_+}$ then there may not be an ESS reachable from $(1, t_{\mathrm{min}})$.

So far it has been assumed that the variance, in the phenotypic expression of the male handicap trait is fixed. In some circumstances it may be appropriate to consider this trait to be able to evolve freely, in a manner similar to q, n and t. In Example 2, the arguments that show that a population playing (n, t) can be invaded by a handicap trait of marginally higher mean, can easily extended to show that populations playing (n, t), can be invaded by a male strategy t' which give rise to flat phenotype distributions of width w with mean t', provided w and t'satisfy the conditions that w is only marginally less than 1 and $t' + w/2 = t + 1/2$. Once such a handicap trait has invaded, a trait with slightly smaller phenotypic distribution width than w can invade, and so on. That is, in Example 2 there is selection pressure for canalisation of the male handicap trait. This conclusion is of course case specific, as examples can be constructed in which the opposite occurs (cf. Pomiankowski & Møller 1995).

9.9 Comparison with the Strategic Handicap

The above model is a counterpoint to the strategic handicap model of Grafen (1990a) and the strategic signalling models presented in the first part of this thesis. There are several points of interest that should be noted.

First, in Grafen's model, trait development is as quality sensitive as possible—the ESS is calculated under the assumption that the strategy is a function of quality. In the epistatic model outlined above, the level of trait development is independent of an individual's quality. Thus, the above model and Grafen's model represent the two extremes of the range of developmental sensitivity of handicaps. ESSs, at which traits are exaggerated and females are discriminating, exist in both models. It is reasonable, therefore, to conclude that developmental sensitivity is immaterial to the functioning of the handicap principle. In a sense then, the epistatic mechanism is the more basic of the two mechanisms; it makes precisely one less assumption than the strategic handicap mechanism. Developmental sensitivity was first mentioned in reference to the handicap principle in Zahavi (1977), and all successful models since then have made this assumption in some form. This model shows that Zahavi's original argument (Zahavi 1975) is viable without needing recourse to conditional development of the handicap trait.

Second, the precise mechanisms of female choice differ between Grafen's model and the epistatic model here. This is insignificant. The pool-comparison method was used here because it was easy to illustrate various points with it; the relative mating success of a male being given by $x^{n-1}(a, t)$. The general results presented here still follow if x^{n-1} is replaced by an arbitrary strictly increasing function of x. In particular, Grafen's model of female discrimination could have been used (with some minor reinterpretation). Conversely, Grafen's (1990a) results can be repeated for the situation in which females choose the best of n, or almost any other model of female discrimination (see chapters 2 to 7).

Third, the inclusion of environmental variance in the development of the trait is necessary for the above epistatic model to work, as there must be some variance in the male trait for female preference to be exhibited. Grafen assumed that there was no error in development. If, however, he had assumed environmental variance in development of the trait which was uncorrelated with quality, then there would have been an obvious way in which to view the strategic handicap as a refinement of the epistatic handicap. The trait genotype t in the above epistatic model and strategies in Grafen's model in which the expectation value of advertising is independent of q and equal to t would be identical.

This provides a nice way of conceptualizing the first point made above. In the epistatic handicap, the set of possible strategies is identical with the subset of constant functions, denoted U_0. In the strategic handicap, the set of possible strategies is assumed to be identical with the set of all functions of quality. It may be shown, however, that the only functions that are possible ESSs are increasing (Grafen 1990a; chapter 2 this thesis); denote the set of these by U_∞. Between these two extremes lie conditional handicap models in which the strategy set is larger than the epistatic handicap, but still restricted; denote these by U_α. Set inclusion then defines a partial ordering on these models; in particular:

$$U_0 \subset U_\alpha \subset U_\infty$$

The final point to be made pertains to the observation that 'survival' must satisfy the same conditions in the epistatic handicap as in the strategic handicap model of Grafen (1990a). In both epistatic and strategic handicap models, equation (9.2) guarantees that there is a correlation between the level of trait observed by females during the breeding season and the trait bearer's quality. However, this correlation is induced by two different mechanisms. In the strategic handicap, the condition allows males of high quality to advertise at a higher level than low quality males because doing so is cheaper, in terms of survival, for them. In the epistatic model, the effect of the condition is to correlate actual quality and the phenotypic level of trait indirectly by the differential survival of males of different qualities. In strategic handicap models with error in development of the trait, both effects of the condition come into play (see sections 4.1 and 5.4).

10 Quantitative Genetics and Correlations

10.1 Motivation and Outline of Chapter

Recently, Iwasa et al. (1991) have adduced a quantitative genetics model to show that the epistatic handicap principle does not work. The lynch-pin of their argument is the assumption that, at equilibrium, the correlation between the viability genes and the genes affecting female discrimination (ρ_{pv}) is indirect, coming solely from the correlation between the male trait and viability (ρ_{tv}) and the male trait and female discrimination (ρ_{pt}) directly induced by natural selection and the effects of female choosiness respectively. This, they claim, implies that:

$$\rho_{pv} = \rho_{pt}\rho_{tv} \tag{10.1}$$

This argument has been repeated by Møller (1994).

In the following sections, three models are provided to show the invalidity of this conclusion. The first two models show that environmental and non-additive genetic variance, whilst not affecting the change in mean of a trait in a quantitative genetics model given the additive genetic variances and covariances, cannot be ignored when calculating equilibrium genetic covariances.

The third model is a complete major gene model of the epistatic handicap process. This model shows that, regardless of the effects of environmental and non-additive genetic variance, the argument leading to equation (10.1) is flawed as it does not take into account the effects of mutation and recombination on covariances (cf. Barton & Turelli 1991).

It would have been preferable to exhibit the flaw in the logic which results in equation (10.1) with by a simple reanalysis of Iwasa et al.'s model, perhaps with a few additions (such as environmental variance). However, this proved to be analytically untractable. In any case, as there are two distinct flaws in their reasoning, distinct analyses of each flaw are perhaps appropriate.

10.2 A Hybrid Q.G. Model

In this section a hybrid quantitative genetics/major gene model is considered, the purpose of which is to suggest that environmental and non-additive genetic variance cannot be disregarded in calculating equilibrium genetic correlations. The assumption that environmental variances may be ignored when calculating genetic covariances is a crucial assumption by Iwasa et al. (1991) in their arguments against the epistatic handicap mechanisms.

It is assumed, like Iwasa et al. (1991), that female discrimination and individual viability are polygenic traits, and that there is constant supply of additive genetic variance in these traits due to, *inter alia*, mutation and recombination. Unlike Iwasa et al., it is assumed that the male trait is controlled by a single locus. That the male trait is treated differently from viability and female preference is an unwelcome assumption; it would have been preferable to have both additive genetic and environmental variance, but this has proven too difficult. However, not including additive genetic variance in the male trait has its positive points—any female choosiness at equilibrium can only be due to benefits obtained by mating with males of higher quality.

As well as showing how environmental (and/or non-additive genetic) variance may lead to the stable evolution of epistatic handicaps, this model also provides confirmation of the results of the continuous game theory model of the previous section. The similarities between the results are noted as they occur.

Familiarity is assumed with the notation of Iwasa et al. (1991), which is similar to that found in Lande (1980,1981). The same assumptions about mutation bias are made, and the same female fitness function is used. The only difference is that it is assumed that the male trait is determined by a single major gene and the evolution of the male trait is analysed in terms of whether a population of males all bearing the same major trait gene can be invaded by a mutant bearing a different major trait gene. It is assumed that male zygotes bearing a major trait gene, t, develop a preselection distribution of trait phenotypes of mean t and non-zero variance. Phenotypic fitness, $W_m(a, v)$ of a male of genetic viability v and trait phenotype a is partitioned into two components:

$$W_m(a, v) = W_d(a) W_n(a, v)$$

where W_d represents the component of fitness due to female discrimination, and W_n the effects of viability and bearing of the trait on survival. It is assumed that the effects on the fitness of males of bearing a trait of phenotype a satisfy:

$$\frac{\partial}{\partial a}\left(\frac{\partial \ln[W_n(a, v)]}{\partial v}\right) > 0 \qquad (10.2)$$

The above equation is identical to equation (9.2) with a strict inequality. It implies that the mean viability of males is increasing in the level of the trait that they bear, which is a sufficient condition for the evolution of female choice when there is no additive genetic variance in the trait.

Noting the argument in the appendix of Iwasa et al. (1991) that shows that the same equations govern the change in genetic mean as govern the change in phenotypic mean, the change in mean phenotype of intensity of female discrimination, p, and mean viabiliy of offspring, v, between generations is given by:

$$\begin{pmatrix} \Delta\bar{p} \\ \Delta\bar{v} \end{pmatrix} = \frac{1}{2}\begin{pmatrix} G_p & B_{pv} \\ B_{pv} & G_v \end{pmatrix}\begin{pmatrix} \partial \ln W_f/\partial p \\ \partial(\ln W_m + \ln W_f)/\partial v \end{pmatrix} + \begin{pmatrix} 0 \\ -w \end{pmatrix}$$

Assuming the same female fitness function as Iwasa et al., a simple calculation yields:

$$\bar{p}_{eq} \propto \frac{wB_{pv}}{b \mid G \mid}$$

where w is the effect on the genetic mean due to mutation bias, per generation. Note that in this equation $\bar{p}_{eq}$ is inversely proportional to the parameter b which is a measure of the cost of discrimination. That is, the cheaper it is to be discriminating, the more discriminating females will be. This, unsurprisingly, is similar to the game theory model of the previous section.

The only thing left to consider is the value of B_{pv}, the equilibrium additive genetic covariance between preference and viability. Equation (10.2) implies that the genetic viability of adult males is correlated with increasing trait level. The more discriminating a female the more likely she is to mate with a male bearing a phenotypic trait of large size relative to the rest of the population. Thus, she is more likely to choose a male of high relative genetic viability and, therefore, B_{pv} must be positive at equilibrium, even if the correlation between the trait and viability is purely epistatic.

To complete the model all that needs to be considered is whether a male trait genotype, t, and the corresponding covariance of viability and female discrimination $B_{pv}(t)$ is an ESS, or, less strictly, is locally stable against invasion of a new genotype t' This will be highly case specific, like the game theory model of the previous section, and so is not attempted here. Depending upon the functional relationship between t and B_{pv} and the relationship between mean level of female discrimination and relative male fitness, all the possibilities outlined in the continuous game theory model are possible, including the existence of multiple ESSs or non-existence of an ESS.

The important point is, however, that regardless of the male trait ESS, the equilibrium level of the mean level of female discrimination is always positive and non-zero, contrary to the result of Iwasa et al. (1991). I would suggest that, if the calculation could be performed, the inclusion of environmental variance would invalidate the argument induced by Iwasa et al. (1991) to reject the epistatic handicap. Whether this is true or not, the computational model, exposited later, shows that there is a simpler and distinct reason why equation (10.1) is false in the case of the epistatic handicap mechanism.

10.3 The Effects of Non-Additive and Environmental Variance on Additive Genetic Covariances and Intensity of Selection

It is a standard result (Bulmer 1980, Falconer 1989, Iwasa et al. 1991) that, when calculating the change in mean of a trait between generations in a quantitative genetics model, the effects of environmental and non-additive genetic variances may be ignored; all that is required is a knowledge of the additive genetic variances and covariances. However, environmental and non-additive variances and covariances cannot be ignored when calculating equilibrium values of genetic covariances as the following simple sexual selection example shows. The model is not intended to be a realistic model of sexual selection; it has been constructed only to clearly illustrate the interaction between environmental variance and genetic correlation.

Consider a population of haploid semelparous individuals. Initially assume at one locus 50% of the population carry an allele p_0 and the other 50% carry p_1. At another locus 50% carry t_0 and 50% carry t_1. The t-locus controls the development of an ornament. Males bearing t_1 on average bear larger ornaments than males bearing t_0. The p-locus controls female choice. Females bearing p_0 prefer males with small ornaments, females bearing p_1 prefer males bearing large ornaments. The female search strategy is as follows: randomly sample two males, if of genotype p_1 mate with the male bearing the largest trait, if of genotype p_0 mate with the male bearing the smallest trait, unless the preferred male's phenotype cannot be of the preferred genotype, in which case females sample another two males. If both males bear traits of equal size, sample another two males. To simplify analysis, it is assumed that there is no cost arising from being discriminating, there is no cost for bearing a trait, and all matings produce the same number of offspring. The two loci are assumed to segregate independently and there are assumed to be no interactions between the loci in the determination of the phenotype.

Assume that each of the male trait genotypes, t_i, give rise to phenotypes with flat distribution of width w centred on i. The frequency of the genotype (p_i, t_j) at the nth generation will be represented by f_n^{ij} From the previous paragraph:

$$\begin{aligned} f_0^{i0} + f_0^{i1} &= \frac{1}{2} \\ f_0^{0i} + f_0^{1i} &= \frac{1}{2} \end{aligned}$$

and assume further that:

$$f_0^{10} = f_0^{01}$$

By symmetry, the above three relationships hold for all n. Noting this, a tedious calculation provides the following recurrence relations for the frequencies of the genotypes:

$$\begin{aligned} f_{n+1}^{ii} &= (2a-1)(f_n^{ii})^2 - a f_n^{ii} + \frac{1}{4}a \\ f_{n+1}^{ij} &= \frac{1}{2} - f_{n+1}^{ii} \qquad i \neq j \end{aligned}$$

where:

$$a = \begin{cases} 1 & w \leq 1 \\ \frac{2w^2+2w-1}{4w^2-2w+1} & w \geq 1 \end{cases}$$

The equilibrium values of f^{ij} are then:

$$\begin{aligned} f^{00} = f^{11} &= \frac{a - \sqrt{a - a^2}}{4a - 2} \\ f^{01} = f^{10} &= \frac{1}{2} - \frac{a - \sqrt{a - a^2}}{4a - 2} \end{aligned}$$

Simple calculations show that the additive genetic variance at the p-locus is $G_p = \frac{1}{4}$. The additive genetic variance at the t-locus is $G_t = \frac{1}{4}$. However, the genetic covariance between the two loci, B_{pt}, and hence the correlation ρ_{pt} is dependent upon a and hence the environmental variance. Precisely:

$$\begin{aligned} B_{pt} &= \frac{a - \sqrt{a - a^2}}{4a - 2} - \frac{1}{4} \\ \rho_{pt} &= \frac{4a - 4\sqrt{a - a^2}}{4a - 2} - 1 \end{aligned} \tag{10.3}$$

This should be expected, as changing w is equivalent to changing the intensity of the female preference which would also have effects on the equilibrium correlation. In particular, note that for extremely 'strong' selection (i.e. $w \leq 1$), $\rho_{pt} = 1$, and for extremely weak selection (i.e. $w \gg 1$) $\lim_{w \to \infty} \rho_{pt} = 0$.

10.4 Three Locus Computational Model

The following model is a complete model of sexual selection under the epistatic handicap mechanism. However, it does not exclude the Fisher process. This is unimportant, as the purpose of the model is not to show that the episttic handicap mechanism can function by itself, this is shown by the models of sections 2 and 3.1, but to show that the argument of Iwasa et al. (1991) leading to equation (10.1) is flawed. It should be noted that their argument is not peculiar to quantitative genetics— and thus it may be investigated by a major gene model.

10.4.1 Description of Model

The model is three locus haploid, with no chromosomal linkage between the loci. One locus controls the viability or quality of individuals, represented by v. The second locus represents the level of expression of the handicap trait in males, represented by t. The final locus represents the intensity of preference of females, represented by p. Females are assumed to use a pool comparison rule as described in the continuous game theory model. In the first instance, alleles at the t and p loci are assumed not to affect the direct fitness of males and females respectively. The species is assumed to be semelparous, with males and females breeding with individuals of their own cohort. Population size is assumed to be large enough so that stochastic and discrete population size effects can be ignored.

Alleles are ordered in terms of increasing intensity. Thus, v_0 is the lowest viability, v_1 has higher survival that v_0 but less than v_2•etc. Similarly, the effect of t_i on survival is less than the effect of t_{i+1}; t_0 is assumed to have no effect on survival. Each of the p_i is associated with an n_i which are the size of the sample of males from which they choose. $n_i < n_{i+1}$ and one of the n_i is equal to zero and thus females of the associated p genotype do not discriminate. The cost to survival of p_i is assumed to be increasing in i.

The temporal order of events in the model is as follows:

1. **Birth:** Determination of the sex of individuals at birth is assumed to be independent of the three loci under consideration. In the first generation the distribution of juvenile genotypes, $G_j(p, t, v)$ is assumed. The $G_j(p, t, v)$ in

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subsequent generations are calculated from the effects of selection, differential mating success, and mutation on the previous generation (see steps (2-4) below).

2. **Selection:** Selection is assumed to occur between birth and mating. The frequency of the genotype (p, t, v) in males after selection is assumed to be given by:

$$G_m(p,t,v) = \kappa_m G_j(p,t,v) S_t(t,v) S_v(v)$$

   where $S_t(t,v)$ is the effect on survival on an individual of viability v bearing a trait of size t; $S_v(v)$ is the direct effect of viability on survival, and κ_m is a normalizing constant. Note that as S_t is a function of both t and v there is the possibility of interaction between the trait and viability on survival. The distribution of female genotypes after selection is assumed to be given by:

$$G_f(p,t,v) = \kappa_f G_j(p,t,v) S_p(p) S_v(v)$$

   where $S_p(p)$ is the effect on survival, due to being discriminating at intensity p, and κ_f ia a normalizing constant.

3. **Mating:** Females are then assumed to select mates from randomly sampled pools of surviving males. For one allele at the p-locus it is assumed that the pool size is 1, i.e. females carrying this allele are not discriminating. Males are assumed to be able to mate as often as they like. All females are assumed to produce the same number of zygotes. Zygotes inherit the allele that they bear at each locus with equal probability from their mother or father. Inheritance is independent at each locus. Zygotic gene frequencies are labelled $G_z(p,t,v)$.

4. **Mutation:** It is assumed that for each zygote there is a chance that each allele that has combined to form it has mutated. Mutations are assumed to either increase or decrease the allele by one step in the ordering, i.e. $x_i \rightarrow x_{i+1}$ or $x_i \rightarrow x_{i-1}$. To keep the number of alleles finite, it is assumed that the maximal and minimal alleles cannot increase or decrease respectively. For each allele the transition probability 'up' is represented by $M^+(x_i)$ and the probability that an allele will decrease is represented by $M^-(x_i)$. As the model assumes large population size, it is assumed that precisely the proportion $M^\pm(x_i)$ undergo transition. The sum total of mutations gives $G_j(p,t,v)$ for the next generation from G_z.

The listing of the QBASIC program for this model can be found in Appendix D. Numerous simulations were run; and an example of a stable state reached is given in Table 3. At each generation, the means of each locus, and pairwise correlations between loci were calculated for each of G_f, G_j, G_m, and G_z and are represented by the notation μ^{type}_{locus} and $\rho^{type}_{locus1,locus2}$ respectively, e.g. the correlation between p and v for G_z is represented by ρ^z_{pv}. The weighting of allele x_i for these calculations was set at i. Equilibrium was reached when all the G were constant between generations. For each model the mutational equilibrium and mutational viability equilibrium were also calculated to highlight the effects of sexual selection.

Model Parameters	
No. of Alleles	$\mid p \mid = 5, \quad \mid t \mid = 3, \quad \mid v \mid = 2$
$n(p)$	$[\ 0.5 \quad 0.75 \quad 1 \quad 1.5 \quad 2\ ]$
$S_p(p)$	$[\ 0.99 \quad 0.999 \quad 1 \quad 0.999 \quad 0.99\ ]$
$S_t(t, v)$	$\begin{bmatrix} 1 & 1 \\ 0.95 & 0.99 \\ 0.90 & 0.98 \end{bmatrix}$
$S_v(v)$	$[\ 0.5 \quad 1\ ]$
$M_p^-(p)$ $M_p^+(p)$	$[\ 0.00 \quad 0.01 \quad 0.01 \quad 0.01 \quad 0.01\ ]$ $[\ 0.01 \quad 0.01 \quad 0.01 \quad 0.01 \quad 0.00\ ]$
$M_t^-(t)$ $M_t^+(t)$	$[\ 0.00 \quad 0.05 \quad 0.05\ ]$ $[\ 0.05 \quad 0.05 \quad 0.00\ ]$
$M_v^-(v)$ $M_v^+(v)$	$[\ 0.00 \quad 0.20\ ]$ $[\ 0.01 \quad 0.00\ ]$

Gene Pool	Equilibrium Values
G_f	$\rho_{pv} = 3.195 \times 10^{-4} \quad \rho_{pt}\rho_{tv} = 4.069 \times 10^{-5}$ $\mu_p = 3.195 \quad \mu_t = 1.841 \quad \mu_v = 0.766$
G_m	$\rho_{pv} = 7.941 \times 10^{-4} \quad \rho_{pt}\rho_{tv} = 5.168 \times 10^{-5}$ $\mu_p = 3.198 \quad \mu_t = 1.839 \quad \mu_v = 0.780$
G_z	$\rho_{pv} = 5.422 \times 10^{-4} \quad \rho_{pt}\rho_{tv} = 1.023 \times 10^{-4}$ $\mu_p = 3.203 \quad \mu_t = 1.886 \quad \mu_v = 0.773$
G_j	$\rho_{pv} = 3.664 \times 10^{-4} \quad \rho_{pt}\rho_{tv} = 4.665 \times 10^{-5}$ $\mu_p = 3.198 \quad \mu_t = 1.842 \quad \mu_v = 0.621$

Gene Pool	Equilibrium Values (Random Mating)
G_f	$\mu_p = 2.000 \quad \mu_t = 0.892 \quad \mu_v = 0.760$
G_m	$\mu_p = 2.000 \quad \mu_t = 0.879 \quad \mu_v = 0.767$
G_z	$\mu_p = 2.000 \quad \mu_t = 0.886 \quad \mu_v = 0.763$
G_j	$\mu_p = 2.000 \quad \mu_t = 0.891 \quad \mu_v = 0.613$

Gene Pool	Equilibrium Values (Mutation Only)
G_j	$\mu_p = 2.000 \quad \mu_t = 1.000 \quad \mu_v = 0.048$

Table 3: *Equilibrium values of sample run of computational model of epistatic handicap mechanism. Female preference* $n(p) < 1$, *indicates that females bearing p allele prefer males with low t. Note that although* M_v *is directional in this simulation, it is not a necessary condition. This equilibrium was reached by both, simulations which started with all indiviuals being, with equal frequency, either genotype* $(2, 0, 0)$ *or* $(2, 0, 1)$, *and simulations which started with equal frequencies for all alleles. Results of an equivalent model which disregarded assortative mating, and a model which solely considered the mutational equilibrium are given; both of these simulations started with equal frequencies for all alleles.*

10.4.2 Results and Comments

The most important result of the simulations is that at equilibrium the covariances between the loci did not satisfy equation (10.1) as they should if Iwasa et al.'s (1991) assumption about equilibrium additive genetic correlations was correct. (It should be stressed that Iwasa et al.'s argument is not specifically a quantitative genetic's argument.) Perusal of the difference in equilibrium correlations between the pre- and post-mutation zygotic, male, and female gene pools given in Table 3 shows why: recombination and mutation both alter the relationship between ρ_{pv} and $\rho_{pt}\rho_{tv}$. In particular, the difference between ρ_{pv} and $\rho_{pt}\rho_{tv}$ is roughly the same order of magnitude as ρ_{pv}. This is to be expected as at equilibrium the correlating effects of selection are exactly balanced by the uncorrelating effects of mutation and recombination. The effect of recombination on correlations can be quite large; in a population mating at random, the effect of recombination on unlinked loci is to reduce linkage disequilibrium by a factor of $\frac{1}{2}$ per generation (Falconer 1989).

There is one situation in which the logic of Iwasa et al.'s (1991) argument does hold: If there is no mutation and juveniles inherit their allele at the t- and v-loci from their fathers and their p- allele from their mothers, then equation (10.1) holds for every generation provided that the population starts in a condition in which the equation is true (e.g. linkage disequilibrium). This was tested computationally, and equation (10.1) was satisfied for a number of generations, until rounding errors began to distort the results.

The model was run with various numbers of alleles, various costs of discrimination and trait, and various starting distributions of alleles, and in general equilibria which were obtained differed in the expected direction from the random mating equilibrium. Similar results also obtained when females developed the costly trait.

It should be noted that the computational model does not exclude Fisherian effects. When the number of viability alleles is reduced to one, the model becomes one of the Fisher process. A Fisher process model with similar parameters to those in Table 3 had similar equilibrium. The point of this model was not to show that the epistatic handicap mechanism worked without Fisherian effects, this has been shown by the non-computational models, but that the indirect correlation argument adduced against the epistatic mechanism is flawed.

In addition to use in 'rejecting' the epistatic handicap mechanism, the argument that indirect genetic correlations are equal to the product of the relevant direct correlations has been used by Pomiankowski & Iwasa (1993) and Iwasa & Pomiankowski (1994) in other models of sexual selection.

The effect of this assumption on Pomiankowski & Iwasa (1993) is minor; it only effects equation (12), but not the result derived from this. The effect on the conclusions of Iwasa & Pomiankowski (1994) is more substantial. The above assumption is central to the derivation of the slow dynamics in Appendix A of Iwasa & Pomiankowski (1994) which implies equations (9), (10a), (10b), (15), and (16), which are the core results of the paper, as they described the equilibrium values of intensity of female preference, are flawed at least in detail.

Finally, the computational model highlights a distinction between two definitions of mutation bias, which does not appear in quantitative genetic models (Pomiankowski et al. 1991). Pomiankowski et al. (1991) have quite correctly pointed out that for an equilibrium to exist in a model in which there is directional selection on a trait, such as is the case in many models of sexual selection, the effect of mutation (or any other force that supplies additive genetic variance) must be in the opposite direction of the effect of selection. In fact, for an equilibrium to exist these two forces must be precisely balanced. To put this another way, if selection increases the mean of a trait by an amount $\Delta\mu$ each generation and decreases the amount of additive genetic variance by Δv, then for the sys-

Model Parameters for Positive Mutation Bias	
$M_v^-(v)$ $M_v^+(v)$	$[\ 0.00\ \ 0.10\ ]$ $[\ 0.20\ \ 0.00\ ]$
Gene Pool	Equilibrium Values
G_j	$\rho_{pv} = 1.624 \times 10^{-4}$ $\rho_{pt}\rho_{tv} = 2.166 \times 10^{-5}$ $\mu_p = 3.194$ $\mu_t = 1.842$ $\mu_v = 0.842$

Model Parameters for Zero Mutation Bias	
$M_v^-(v)$ $M_v^+(v)$	$[\ 0.00\ \ 0.20\ ]$ $[\ 0.20\ \ 0.00\ ]$
Gene Pool	Equilibrium Values
G_j	$\rho_{pv} = 2.107 \times 10^{-4}$ $\rho_{pt}\rho_{tv} = 2.810 \times 10^{-5}$ $\mu_p = 3.196$ $\mu_t = 1.842$ $\mu_v = 0.696$

Table 4: *Sexual selection equilibria when mutation is biased in favour of high quality genes, and when mutation is unbiased. The rest of the parameters are identical to those that appear in Table 3. Note the similarity between equilibrium values of p and t for the models described by the sets of parameters in this table and the model described in Table 3, which confirms that the equilibria in these examples are mainly supported by the Fisher process.*

tem to be in equilibrium, another force must decrease the mean by an amount $\Delta\mu$ and increase the additive genetic variance by an amount Δv. Pomiankowski et al. (1991) have called this observation mutation bias. This conception of mutation bias is *not* equivalent to the intuitive notion that a mutation in a gene is more likely to decrease its fitness than to increase its fitness, and equilibria may exists in circumstances when the effect of mutation is, on a gene by gene basis, expected to be beneficial. Two examples illustrating this are given in Table 4. In the first of these examples, mutation between low and high 'quality' genes is twice as high as in the opposite direction. In the second example the chance of mutation between the two states is equal. Note, however, that in both cases the effect of mutation on the mean quality of individuals is negative because there are more high quality individuals than low quality individuals in the population.

10.5 Discussion

The epistatic handicap principle has been previously rejected as untenable for three theoretical reasons. The first reason, adduced as an argument against the handicap principle in general, arises from Fisher's Fundamental Theorem of Natural Selection (Fisher 1930) which states that, at equilibrium, there should be no additive genetic variance in traits that affect fitness. This implies that females could not be selecting males for their good genes because the additive genetic variance which affects fitness is zero. There are at least two responses to this.

First, this argument does not prevent handicap mechanisms from working on environmental variances in qualities that are direct of interest to females, such as foraging ability in the case where males help raise young (Heywood 1989). Second, the assumptions on which Fisher's result are based probably do not hold. It has been estimated that at equilibrium mutation may provide a fair amount of additive genetic variance in fitness (Charlesworth 1987; Kondrashov

1988; Rice 1988), though this should be tempered by the observation that large amounts of enviromental variance may reduce the ability of females to select the best mates (see model above). Further, it might be argued that populations may never be in a static equilibrium, due to spatial heterogeneity of physical or biological environments coupled with dispersion (cf. Tangled Bank hypotheses: Ghiselin 1974, Williams 1975, Bell 1982), temporal heterogeneity of physical environments, or Red Queen (Van Valen 1973) effects: changing biological environments due to the co-evolution of competitors, parasites (Hamilton & Zuk 1982), predators and prey.

The second argument that has been levelled at the epistatic handicap is that for the mechanism to work the fitness advantage of inheriting high viability genes must be much greater than the cost of bearing a large handicap (Davis & O'Donald 1976; Maynard-Smith 1976). Where the number of zygotes a male produces is independent of the size of trait that he bears, this is a strong argument against the epistatic mechanism. This is because the benefit that is gained by a discriminating female is due entirely to the correlation between the trait borne by a male and his viability due to differential survival and this benefit comes at a cost to her sons in their decreased survival because they are likely to inherit the trait. If the differential effects are small, then so will be the correlation between trait and viability: thus the only situation in which the conditions necessary for the epistatic process can apply is when there is differential selection amongst the types due to the trait being much stronger than the cost of the trait to the best males relative to the natural selection optimum (cf. Eshel 1978, Andersson 1982). This seems unlikely. Even if this was the case, assortative mating between females of high viability and males with large traits would have to be particularly strong for females not to have reductions in their fitness due to producing sons with a low chance of survival due to them, on average, inheriting the mean genetic viability of their father and mother coupled with a costly trait from their father.

The possibility of males surviving to the mating season obtaining more than the mean number of offspring was removed from the early models of the handicap principle so as to avoid the possibility that a sexual selection equilibrium obtained was not due to handicap mechanisms, but to the Fisher process. However, this is not the only way by which the Fisher process may be excluded from models of sexual selection. Another way is to look for equilibria in which there is no additive genetic variance in the trait genotype.

Case 2 of Example 2 of the game theory model in section 2 shows that if the direct cost to females of being discriminating is small relative to the benefits gained by an increased chance of mating with a male of higher viability, an equilibrium can exist in which the survival of males is significantly reduced and females discriminate. Female discrimination is still selected for at the end of the runaway process because it provides females with benefits due to choosing males of high viability. If there was no interaction between the cost of bearing a trait and viability in males, that is in the pure corresponding Fisher runaway selection model, the only equilibrium obtainable is the one in which the male trait genotype is at its natural selection optimum and no female discriminates. Thus the effects of the epistatic handicap mechanism on the results of Fisherian runaway selection may be more than the subtle effects noted by some authors (e.g. Bell 1978).

The third argument against the epistatic handicap principle alleges that it cannot work because at equilibrium the intensity of female preference is proportional to the additive genetic correlation of female preference and male trait minus the product of the correlation between the preference and viability genes and the correlation between the trait and viability genes, i.e. equation (10.1). This, Iwasa et al. (1991) argue, must be zero in the case of epistatic handicaps as ρ_{pv} arises indirectly and solely through the direct correlations ρ_{pt} and ρ_{tv}.

The models presented here suggest two reasons why this is not the case. The first is that the effects of environmental and non-additive genetic covariances have not been taken into account. The second is that the argument ignores the significant effects of mutation and recombination on genetic variances and covariances. The only case in which Iwasa et al.'s argument works is when variance in the traits is due to additive genetic variance, there is no mutation, inheritance of preference is solely through the female line, and inheritance of viability and trait is solely from the male. These conditions seem rather unreasonable.

Whether or not there are any pure epistatic handicap traits in nature is not a matter that can be decided from an ergonomic chair. However, the models presented here have shown that the epistatic handicap mechanism could indeed work. Further, they illuminate the connection between the epistatic and strategic handicap mechanisms. Finally, the models raise important questions about the the validity some certain results appearing in Iwasa et al. (1991) and Iwasa & Pomiankowski (1994).

III

Appendices

A An Existence and Uniqueness Theorem

In Proposition 2.1 a global existence and uniqueness result for the solution of a non-autonomous non-linear differential equation that is only satisfied almost everywhere is used. In this appendix I prove such a theorem, as the results that appear in accessible texts on non-linear differential equations rely upon assumptions that are not general enough.

The first problem with the 'standard' results is that they assume that the effect of the independent variable on the equation is continuous. This need not be the case in Proposition 2.1. The second problem is that such theorems are usually stated only as local results. The final problem is that there can never be a uniqueness theorem for a differential equation that is satisfied only almost everywhere, as there exist strictly monotonic continuous functions that are differentiable almost everywhere, and where they are differentiable, the derivative is zero (e.g. Riesz & Nagy 1955 p48). To see why this is so, suppose that $\vec{y}_+$ is one of these strange functions, with $\vec{y}_+(0) = 0$, then if $\vec{y}_\lambda$ satisfies:

$$\frac{d\vec{y}_\lambda}{dx} = \vec{f}(\vec{y}_\lambda + \lambda\vec{y}_+, x) \qquad \text{almost everywhere}$$

with initial condition $\vec{y}(0) = \vec{y}_o$, and where λ is an arbitrary constant, then $\vec{y}_\lambda + \lambda\vec{y}_+$ satisfies:

$$\frac{d\vec{y}}{dx} = \vec{f}(\vec{y}, x) \qquad \text{almost everywhere}$$

with initial condition $\vec{y}(0) = \vec{y}_o$.

What I show in the sequel is that, under certain weak conditions, there exists a unique absolutely continuous function that satisfies the differential equation in question. It turns out that the 'standard' method of proof (successive approximations), may be used to obtain the core of this result, the rest following by application of theorems contained in the analysis text by Riesz & Nagy (1955). Proposition A.1 is, in essence, a restatement of a slightly weaker proposition contained in Struble (1962).

Proposition A.1 *Let $\vec{f}(\vec{y}, x) : \mathcal{R}^n \times \mathcal{R} \to \mathcal{R}^n$ be continuous in $\vec{y}$ for all $\vec{y} \in \mathcal{Y}$ where:*

$$\mathcal{Y} = \{\vec{y}; \|\, \vec{y} - \vec{y}_o \,\| \leq \alpha\},$$

and continuous in $\mathcal{R}^n \times \mathcal{R}$ for almost all $x \in \mathcal{X}$, where $\mathcal{X} = \{x; 0 \leq x \leq \beta\}$. Further assume that:

$$\|\, \vec{f}(\vec{y}, x) \,\| \;\leq\; M(x) \qquad \text{(A.1)}$$

$$\|\, \vec{f}(\vec{y}_1, x) - \vec{f}(\vec{y}_2, x) \,\| \;\leq\; L(x) \,\|\, \vec{y}_1 - \vec{y}_2 \,\| \qquad \text{(A.2)}$$

for all $x \in \mathcal{X}$ and for all $\vec{y}_1, \vec{y}_2 \in \mathcal{Y}$, where $M(x)$ and $L(x)$ are integrable on $\mathcal{X}$. Let β_1 be such that $0 < \beta_1 \leq \beta$ and so that:

$$\int_0^{\beta_1} M(z) \cdot dz \;\leq\; \alpha \qquad \text{(A.3)}$$

$$\int_0^{\beta_1} L(z) \cdot dz \;=\; \delta < 1 \qquad \text{(A.4)}$$

Define a sequence $\vec{y}^{(n)}(x)$ recursively by choosing a function $\vec{y}^{(0)}(x) \in \mathcal{Y}$ continuous for $x \in \mathcal{X}$, and:

$$\vec{y}^{(n+1)}(x) \; = \; \vec{y}_o + \int_0^x \vec{f}(\vec{y}^{(n)}(z), z) \cdot dz \qquad \text{(A.5)}$$

then $\vec{y}^{(n)}(x)$ converges uniformly on $\mathcal{X}$ to a solution of the integral equation:

$$\vec{y}(x) \; = \; \vec{y}_o + \int_0^x \vec{f}(\vec{y}(z), z) \cdot dz \qquad \text{(A.6)}$$

Moreover, this solution, denoted $\vec{y}^{(\infty)}(x)$ is the unique solution on $\mathcal{X}$.

Proof: Equations (A.1), (A.3) and (A.5) imply, via an inductive argument:

$$\| \vec{y}^{(n+1)} - \vec{y}_o \| \leq \int_0^x \| \vec{f}(\vec{y}^{(n)}(z), z) \| \cdot dz \leq \int_0^x M(z) \cdot dz \leq \alpha$$

for $0 \leq x \leq \beta_1$. It should be noted that the integral exists as each component of $\vec{f}$ is a measurable function by pointwise composition of continuous functions and the fact that functions that are continuous almost everywhere and bounded by a measurable function are measurable.

By the triangle inequality:

$$\begin{aligned} \| \vec{y}^{(1)} - \vec{y}^{(0)} \| & \leq \| \vec{y}_o - \vec{y}^{(0)} \| + \int_0^x \| \vec{f}(\vec{y}^{(0)}(z), z) \| \cdot dz \\ & \leq \alpha + \int_0^x M(z) \cdot dz \leq 2\alpha \end{aligned}$$

for $0 \leq x \leq \beta_1$. Applying equations (A.2) and (A.5) we see that

$$\begin{aligned} \| \vec{y}^{(2)} - \vec{y}^{(1)} \| & \leq \int_0^x \| \vec{f}(\vec{y}^{(1)}(z), z) - \vec{f}(\vec{y}^{(0)}(z), z) \| \cdot dz \\ & \leq \int_0^x L(z) \, \| \vec{y}^{(1)} - \vec{y}^{0)} \| \cdot dz \\ & \leq 2\alpha \int_0^x L(z) \cdot dz \leq 2\alpha\delta \end{aligned}$$

Applying the above argument recursively we see that:

$$\begin{aligned} \| \vec{y}^{(n+1)} - \vec{y}^{(n)} \| & \leq \int_0^x L(z) \, \| \vec{y}^{(n)} - \vec{y}^{(n-1)} \| \cdot dz \\ & \leq 2\alpha\delta^{n-1} \int_0^x L(z) \cdot dz \leq 2\alpha\delta^n \end{aligned}$$

for $0 \leq x \leq \beta_1$.

For $n \geq 1$ and $m < 1$ we have, by the triangle inequality:

$$\begin{aligned} \| \vec{y}^{(n+m)} - \vec{y}^{(n)} \| & \leq \sum_{i=0}^{m-1} \| \vec{y}^{(n+m-i)} - \vec{y}^{(n+m-i-1)} \| \\ & \leq 2\alpha \sum_{i=0}^{m-1} \delta^{n+i} \\ & \leq \frac{2\alpha\delta^n}{1-\delta} \end{aligned}$$

where the last inequality is obtained by the fact that the previous sum is bounded by the sum of an infinite geometric series and the fact that this sum is finite and equal to $1/(1-\delta)$ by equation (A.4).

Clearly:

$$\lim_{n\to\infty} \frac{2\alpha\delta^n}{1-\delta} = 0$$

and thus the sequence $\vec{y}^{(i)}(x)$ is Cauchy and uniformly convergent to a continuous function $\vec{y}^{(\infty)}(x)$. Moreover $\| \vec{y}^{(\infty)} - \vec{y}_o \| \leq \alpha$ (otherwise the triangle inequality would lead to a contradiction for some $y^{(n)}$), and $y^{(\infty)}$ satisfies equation (A.6) as

$$\begin{aligned}\int_0^x \vec{f}(\vec{y}(z), z) \cdot dz &= \lim_{n\to\infty} \int_0^x \vec{f}(\vec{y}^{(n)}(z), z) \cdot dz \\ &= \lim_{n\to\infty} \vec{y}^{(n+1)}(x) - \vec{y}_o(x) \\ &= \vec{y}^{(\infty)}(x) - \vec{y}_o(x)\end{aligned}$$

Furthermore, $\vec{y}^{(\infty)}$ is the unique function satisfying the integral equation (A.6), for if $\vec{y}^{(\infty)}$ and $\vec{y}$ both satisfy equation (A.6) then:

$$\| \vec{y}^{(\infty)}(x) - \vec{y}(x) \| \leq \int_0^x L(z) \, \| \vec{y}^{(\infty)}(z) - \vec{y}(z) \| \cdot dz$$

and if d is the least upper bound of $\| \vec{y}^{(\infty)}(x) - \vec{y}(x) \|$ for $0 \leq x \leq \beta_1$:

$$\| \vec{y}^{(\infty)}(x) - \vec{y}(x) \| \leq d \int_0^x L(z) \cdot dz \leq \delta d$$

which contradicts the definition of d. □

Corollary A.2 *Let $\vec{f}(\vec{y}, x)$ satisfy the conditions of Proposition A.1, then there exists a unique function $\vec{y} : [0, \beta_1] \to \mathcal{R}^n$ that is absolutely continuous in each component and satisfies the differential equation:*

$$\frac{d\vec{y}}{dx} = \vec{f}(\vec{y}, x) \qquad \textit{almost everywhere}$$

with the initial condition $\vec{y}(0) = \vec{y}_o$.

Proof: Clearly, $\vec{y}^{(\infty)}$ defined in the previous proposition satisfies the conditions of the proposition by Riesz & Nagy (1955, p48). All we need show is that it is the only such function. To see this, suppose that $\vec{z}$ is absolutely continuous and satisfies the differential equation almost everywhere, then from Riesz & Nagy (1955, p48, p53) we see that, as $\vec{z}$ is absolutely continuous, it is the integral of $\vec{f}(\vec{z}, x)$. □

Proposition A.3 *Suppose that $\vec{f}(\vec{y}, z)$ satisfies the conditions of Proposition A.1, with the added restrictions that $M(x) \leq \mu$ and $L(x) \leq \lambda$ for almost all $x \in \mathcal{X}$ and $\alpha > \beta\lambda$, then the differential equation:*

$$\frac{d\vec{y}}{dx} = \vec{f}(\vec{y}, x) \qquad \textit{almost everywhere}$$

with the initial condition $\vec{y}(0) = \vec{y}_o$, has a unique absolutely continuous solution on $\mathcal{X}$.

Proof: The result follows by dividing $\mathcal{X}$ into subintervals:

$$[0,\beta_1],\ [\beta_1,2\beta_1],\ldots,[n\beta_1,\beta]$$

where $\beta_1 \leq \alpha/\mu, \delta/\lambda$ and applying Corollary A.2 repeatedly, setting the initial condition for the ith interval to be $\vec{y}(i\beta_1)$ from the previous interval. □

B An Important Lemma

The following lemma, in various guises, is used quite often in this paper. The theorem proven in the appendix of Johnstone & Grafen (1992) is a special case of this result; their non-differential condition on the 'perceptual error' function (Johnstone & Grafen 1992, p231) may be shown to be equivalent to the differential condition given in the following lemma, in the same way that Grafen's (1990a) similar condition on survival (α in his notation) can be shown to be equivalent to the differential condition on S used in the multiplicative models in chapter 2. See the discussion of technical difference 2 of section 6.2.1 for further details. One point that should be noted in particular is that Grafen & Johnstone's condition requires that their perceptual error-functions have identical support, which is not required in the following lemma.

Lemma B.1 *Suppose that $R(q)$ is strictly increasing on $\mathcal{Q}$, and that for each p for which the measure of the support (with respect to q) of $u(q,p)$ is greater than zero, where the support (with respect to q) is the interval $[q_\alpha(p), q_\beta(p)]$ where q_α and q_β are increasing functions. Further assume u is absolutely continuous in p on the interior of its support (with respect to (q,p)), and that:*

$$\left(\frac{u_2(q_1,p)}{u(q_1,p)}\right) \leq \left(\frac{u_2(q_2,p)}{u(q_2,p)}\right) \qquad a.e.$$

whenever $q_1 < q_2$ and $e \neq 0$. Then defining:

$$\bar{R}(p) = \int_{q_{\min}}^{q_{\max}} R(q)\frac{u(q,p)}{\bar{u}(p)}f(q)\cdot dq,$$

where $f(q) > 0$ almost everywhere, and where

$$\bar{u}(p) = \int_{q_{\min}}^{q_{\max}} u(q,p)f(q)\cdot dq.$$

$\bar{R}(p)$ is an increasing function of p. Moreover, if there also exist open intervals (q_1,q_2) and (q_2,q_3) both contained in the set of non-zero measure $[q_\beta(p_1), q_\alpha(p_2)]$ so that:

$$\left(\frac{u_2(q_i,p)}{u(q_i,p)}\right) < \left(\frac{u_2(q_j,p)}{u(q_j,p)}\right) \qquad a.e.$$

for almost all $q_i \in (q_1,q_2)$ and $q_j \in (q_2,q_3)$ and almost all $p \in [p_1,p_2]$, then $\bar{R}(p)$ is strictly increasing over $[p_1,p_2]$. This last result holds without the strict inequality of u_2/u if one of q_β and q_α is strictly increasing.

Proof: It is first shown that $\bar{R}(p)$ is increasing in p. Consider:

$$\bar{R}(p_2) - \bar{R}(p_1) \tag{B.1}$$

where $p_2 > p_1$. If $q_\alpha(p_2) \geq q_\beta(p_1)$ then equation (B.1) is greater than:

$$\begin{aligned}
&R(q_\alpha(p_2)) \int_{q_{\min}}^{q_{\max}} \frac{u(q,p_2)}{\bar{u}(p_2)} f(q) \cdot dq - R(q_\beta(p_1)) \int_{q_{\min}}^{q_{\max}} \frac{u(q,p_1)}{\bar{u}(p_1)} f(q) \cdot dq \\
&= R(q_\alpha(p_2)) - R(q_\beta(p_1))
\end{aligned}$$

which is as required.

If $q_\alpha(p_2) < q_\beta(p_1)$ then:

$$\begin{aligned}
\bar{R}(p_2) &\geq R(q_\beta(p_1)) \int_{q_\beta(p_2)}^{q_\beta(p_1)} \frac{u(q,p_2)}{\bar{u}(p_2)} f(q) \cdot dq + \int_{q_\beta(p_1)}^{q_\alpha(p_2)} R(q) \frac{u(q,p_2)}{\bar{u}(p_2)} f(q) \cdot dq \\
&\geq \int_{q_\beta(p_1)}^{q_\alpha(p_2)} R(q) \frac{u(q,p_2)}{\int_{q_\beta(p_1)}^{q_\alpha(p_2)} u(q,p_2) f(q) \cdot dq} f(q) \cdot dq \qquad \text{(B 2)}
\end{aligned}$$

Similarly

$$\bar{R}(p_1) \leq \int_{q_\beta(p_1)}^{q_\alpha(p_2)} R(q) \frac{u(q,p_1)}{\int_{q_\beta(p_1)}^{q_\alpha(p_2)} u(q,p_1) f(q) \cdot dq} f(q) \cdot dq$$

As u is absolutely continuous in p for $(q,p) \in [q_\alpha(p_2), q_\beta(p_1)] \times [p_1, p_2]$,

$$\bar{R}_{(p_1,p_2)}(p) \overset{\text{def}}{=} \int_{q_\beta(p_1)}^{q_\alpha(p_2)} R(q) \frac{u(q,p)}{\int_{q_\beta(p_1)}^{q_\alpha(p_2)} u(q,p) f(q) \cdot dq} f(q) \cdot dq$$

may be differentiated with respect to p on $[p_1, p_2]$ by taking the derivative inside the integral. Setting $g(q,p) = u(q,p)f(q) / \int_{q_\beta(p_1)}^{q_\alpha(p_2)} u(q,p) f(q) \cdot dq$ we obtain:

$$\begin{aligned}
\bar{R}_{(p_1,p_2)}(p) &= \int_{q_\beta(p_1)}^{q_\alpha(p_2)} R(q) \frac{u_2(q,p)}{u(q,p)} g(q,p) \cdot dq \\
&\quad - \int_{q_\beta(p_1)}^{q_\alpha(p_2)} R(q) g(q,p) \cdot dq \int_{q_\beta(p_1)}^{q_\alpha(p_2)} \frac{u_2(q,p)}{u(q,p)} g(q,p) \cdot dq,
\end{aligned}$$

Dropping parameters for notational convenience and noting that R and g are both positive, we see that all that must be shown is that:

$$\int_{q_\beta(p_1)}^{q_\alpha(p_2)} \frac{u_2}{u} \frac{Rg}{\int_{q_\beta(p_1)}^{q_\alpha(p_2)} Rg \cdot dq} \cdot dq - \int_{q_\beta(p_1)}^{q_\alpha(p_2)} \frac{u_2}{u} g \cdot dq \geq 0.$$

Changing the variable of integration to the cumulative distribution function, G, of g we have:

$$\int_0^1 \frac{u_2}{u} \frac{R}{\int_0^1 R \cdot dG} \cdot dG - \int_0^1 \frac{u_2}{u} \cdot dG \geq 0 \qquad \text{(B.3)}$$

Noting that:

$$\int_0^1 dG = \int_0^1 \frac{R}{\int_0^1 R \cdot dG} \cdot dG = 1,$$

and that R is strictly increasing we see that there exists an $s \in (0,1)$ for which:

$$\operatorname{sgn}\left(\frac{R(G)}{\int_0^1 R \cdot dG} - 1 \right) = \operatorname{sgn}(G - s).$$

Define $h(t)$ implicitly by:

$$\int_0^{h(t)} \frac{R}{\int_0^1 R \cdot dG} \cdot dG = \int_0^t dG.$$

To see that $h(t) \geq t$ for all t with equality only for $t = 0$ or $t = 1$ we need to consider two cases:

1. Case $(t \leq s)$:

$$\int_0^t \frac{R}{\int_0^1 R \cdot dG} - 1 \cdot dG < 0.$$

2. Case $(t \geq s)$:

$$\int_t^1 \frac{R}{\int_0^1 R \cdot dG} - 1 \cdot dG > 0.$$

The derivative of with respect to t of:

$$\int_0^{h(t)} \frac{u_2}{u} \frac{R}{\int_0^1 R \cdot dG} \cdot dG - \int_0^t \frac{u_2}{u} \cdot dG. \tag{B.4}$$

is given by:

$$\frac{u_2(h(t))}{u(h(t))} - \frac{u_2(t)}{u(t)} \quad a.e.,$$

and thus the derivative of the l.h.s. of equation (B.4) is non-negative for almost all $t \in (0,1)$ which implies that condition (B.3) holds.

The rest of the lemma follows from minor extensions of the above arguments, which are left to the reader. □

C Generalisations of Thesis Results

The results in this section have been obtained since the thesis viva. They generalise a number of the results obtained in chapter 2 and have been included for completeness. In particular, the generalisation of Proposition 2.4 (Proposition C.2) is important as it may be used to draw links between games that satisfy the single-crossing condition (also known as the sorting, constant- sign, or Spence-Mirrlees condition), Nash's (1950) result concerning the existence of equilibria to strategic-form (also known as normal-form) games, and Glicksberg's (1952) generalisation of Nash's result. Although not done here, Proposition C.2 may be used to solve numerous state- dependent and state independent life-history models. For instance, the results of Leimar (1996) concerning the Trivers-Willard (1973) hypothesis may be generalised to circumstances in which quality is genetically heritable.

C.1 Additive Version of Proposition 2.3

Proposition C.1 *Let* $q_{\max} - q_{\min} < \infty$, *$F$ a strictly increasing absolutely continuous function on* Q *and* $V^pN \in \mathcal{N}(1-5, 7-9)$ *and* V^pN^s *is continuous in*

A. Suppose that $C(A,a,q)$ is continuous in A, and thrice differentiable for all (a,q) for which $C(A,a,q) < \infty$. Also suppose that for all A:

$$\begin{aligned} C_2(A,a,q) &> 0, && \text{(C.1)} \\ \frac{\partial}{\partial q}\left(\frac{C_2(A,a,q)}{V^q(A,q)}\right) &< 0, \textit{for a.a. } (a,q) \textit{ such that } C(A,a,q) < \infty && \text{(C.2)} \end{aligned}$$

and that:

$$\frac{\partial V^p N^s(A,q)}{\partial q} > 0 \quad \textit{for all } A \textit{ and all } q \in Q \qquad \text{(C.3)}$$

Further suppose that for each increasing A, there exists $B(A,q)$ for which $C(A,B(A,q),q) < \infty$ for all q and for which:

$$V^p N^s(A,q_{\max}) - V^p N^s(A,q_{\min}) < \frac{C(A,B(A,q),q) - C(A,a_{\min},q)}{V(A,q)} \qquad \text{(C.4)}$$

and that there exists $B(q)$ which satisfies equation (C.4) for all A (which does not necessarily satisfy $C(A,B(q),q) < \infty$).

Under these of conditions, there exists at least one signalling ESS to the model defined by equation (2.1). Furthermore, any ESS must be strictly increasing and continuous.

Proof: Lemmas 2.1 and 2.3-2.6 may be applied to conclude that any ESS, A^*, must be absolutely continuous and strictly increasing, and that $A^*(q_{\min}) = a_{\min}$.

As has been outlined above, a problem arises when the population structure is allowed to be dependent upon the population signalling strategy, namely the solution to the first order condition for an ESS changes the first order condition; the ESS cannot be simply constructed as the solution to a differential equation, as knowledge of the differential equation requires global knowledge of the ESS. An ESS will be a signalling function that gives rise to the first order condition that generates it. To find such an signalling function requires the use of a fixed point theorem, in this case the theorem due to Schauder (see the proof of Proposition 2.4).

As any ESS to this type of problem must be an absolutely continuous function, the search for an ESS may be restricted to any Banach space that contains these functions, thus set $\mathcal{X}$ to be the Banach space of Lebesgue integrable functions on Q (Riesz & Nagy 1955), which shall be denoted $\mathcal{L}_1(Q)$. Note that the underlying linear-space of $\mathcal{L}_1(Q)$ is not the linear space induced on the set of Lebesgue integrable functions, $L_1(Q)$, by pointwise addition, but the factorspace:

$$L_1(Q)/L_1^0(Q)$$

where $L_1^0(Q)$ represents the subspace of functions that differ from 0 only on a set of measure zero.

Define $B_{\inf}(A,q) \overset{\text{def}}{=} \inf\{a; C(A,a,q) = \infty\}$ and set:

$$\mathcal{S} = \{A;\ A \text{ increasing, and } a_{\min} \leq A(q) \leq B(q) \text{ for all } q \in Q\}$$

Define $M(A)(q)$ to be the unique absolutely continuous solution to the differential equation:

$$\frac{dM(A)}{dq} \overset{\text{def}}{=} \frac{V^q(A,q)(V^p N^s)_2(A,q)}{C_2(A,M(A)(q),q)} \quad \text{a.e.} \qquad \text{(C.5)}$$

with the initial condition $M(A)(q_{\min}) = a_{\min}$. If $A \in \mathcal{S}$, then $M(A)(q)$ exists and is unique by Proposition A.3, as long as it lies within $[a_{\min}, B_{\inf}(A, q)) \times Q$.

It is now shown that $M(A)(q)$ cannot be greater than or equal to $B(A, q)$ on Q' Suppose that $M(A)(q)$ exists for $q \in [q_{\min}, q') \overset{\text{def}}{=} Q'$; $q' > q_{\min}$ by the local result Proposition A.1. Clearly, $M(A)(q)$ is strictly increasing on Q' We may define for all $q \in Q'$ the quasi-payoff function:

$$P_M(A, a, q) \overset{\text{def}}{=} V^p N^s(A, (M(A))^{-1}(a)) - V^p N^s(A, a_{\min}) - \frac{C(A, a, q) - C(A, a_{\min}, q)}{V(q)}$$

Differentiating we obtain:

$$\begin{aligned} \frac{dP_M(A, M(A)(q), q)}{dq} &= \frac{\partial V^p N^s(A, q)}{\partial q} - \frac{C_2(A, M(A)(q), q)}{V(A, q)} \frac{dM(A)}{dq} \\ &- \frac{\partial}{\partial q} \left(\frac{C(A, a, q) - C(A, a_{\min}, q)}{V(q)} \right) \bigg|_{a = M(A)(q)} \end{aligned}$$

The first row of the right hand side of the above equation sums to zero almost everywhere, by the definition of $M(A)$. The second row is positive by equation (C.2) after noting that as C/V is thrice differentiable, we can change the order of differentiation. As $P_M(A, a_{\min}, q) = 0$ for all A and q we can conclude that $P_M(A, M(A)(q), q)$ is non-negative. Hence, $M(A)(q) < B(A, q)$. Furthermore, as $M(A)$ is bounded away from $B_{\inf}(A, q)$, $M(A)(q)$ exists on the entirety of Q. This also implies that $M(A)(q)$ is strictly increasing in q. Thus, M is well defined and sends $\mathcal{S}$ into $\mathcal{S}$.

Clearly, a signalling strategy is a signalling ESS of the model if and only if it is a fixed point of M (see proof of Proposition 2.1 for details).

M is continuous in A, as $V^p N^s$ and S are continuous in A, and M is a compact mapping on $\mathcal{S}$ as $\mathcal{S}$ is compact as it is a closed subset of the set of increasing functions from the closed interval Q to another closed interval $[a_{\min}, B(q)]$ which is compact by Lemma 4 of Grafen (1990a).

It has now been shown that the conditions of Schauder's Fixed Point Theorem are satisfied, and therefore at least one fixed point exists. Any fixed point of M is an ESS. □

C.2 Generalisations of Proposition 2.4

The remainder of this appendix is a sketch of a number of general existence results about equilibria of games that satisfy the single crossing condition. Proposition C.2 and its extension, Proposition C.5 were initially motivated by a desire to show that ESSs existed to models of error-prone signalling analogous to the error-free models of Riley (1979), Mailath (1987), and Grafen (1990a,b). However, the purpose of this document is to show the relationship between Proposition C.5 and Nash's (1950) result on the existence of mixed-strategy equilibria to strategic-form (normal-form) games. It turns out that Nash's result may be obtained by observing that each game in normal form may be arbitrarily closely approximated by a game that satisfies the single crossing condition. This new proof does not rely on Kakutani's Fixed Point Theorem, but on the Schauder-Tychnoff Theorem, and thus the approach may be extended to games in which there are an infinite number of strategies (countable or continuum). For example, although it is not shown here, the same method may be applied to prove the existence of an Nash equilibrium to the War of Attrition (see my thesis for rough details).

C.3 New Notation

The games addressed in this appendix are assumed to be between a finite number of players (as in the Prisoner's Dilemma), a finite number of populations (e.g. males and females in a model of sexual selection), or some combination of players and populations. These players/populations will be labelled by integers and be generically referred to as rôles. Individuals in each rôle may not be identical and will be labelled by a set $Q^{[i]}$, which will in general be referred to as an individual's 'quality', q.

Each rôle will be assumed to be able to choose its strategy, $A^{[i]}(q)$, from a set $\mathcal{A}^{[i]}$. It will be assumed that $A^{[i]}(q)$ is a function of q, though the results presented below hold, *mutatis mutandis*, under the assumption that $A^{[i]}$ assigns a distribution of strategies from $\mathcal{A}^{[i]}$ to each q. It may appear, at this stage, that this assumption precludes the consideration of mixed strategies. This is not the case, but a discussion of how this is done will be left to a more appropriate section in the paper. The strategy state of the entire population (i.e. the sum of all rôles) may then be described by a vector $(A^{[1]}, A^{[2]}, \ldots, A^{[n]}) \stackrel{\text{def}}{=} \vec{A}$.

The cumulative distribution of individual qualities in rôle i is represented by $F^{[i]}(\vec{A}, q)$, and the cumulative distribution over all rôles by $\vec{F}(\vec{A}, q^{[1]}, q^{[2]}, \ldots, q^{[n]})$. The associated probability distributions (i.e. the functions to which the $F^{[i]}$ are primitive) are denoted by $f^{[i]}(\vec{A}, q)$.

The payoff to an individual in rôle i, of quality $q^{[i]}$ playing a strategy $a^{[i]}$ is represented by $P^{[i]}(\vec{A}, a^{[i]}, q^{[i]})$. In accordance with the notation outlined for strategies $(P^{[1]}, P^{[2]}, \ldots, P^{[n]}) \stackrel{\text{def}}{=} \vec{P}$. The notation $\vec{q}$, $\vec{a}$ should be interpreted in the obvious manner, $\vec{\mathcal{A}}$ represents the space $\mathcal{A}^{[1]} \times \mathcal{A}^{[2]} \times \ldots \times \mathcal{A}^{[n]}$, and $\vec{\mathcal{Q}}$ should be interpreted similarly.

It should be noted that the notation and hence arguments used in sections [9]-[11] of the proof of Proposition C.2 are slightly informal as I have yet to work out the best way of presenting this argument. In particular, it should be noted that a_{inf} and a_{sup} are functions on $\vec{\mathcal{A}} - \mathcal{A}$ and not constants. This is made reasonably clear in the proof of Proposition C.2, but may not be so clear where they are used elsewhere in this appendix.

The equilibrium definitions of section 1.7 may be extended to global equilibrium concepts (i.e. ones in which all the rôles' strategies are allowed to vary independently) in the obvious manner. For example: a strategy $\vec{A}^*(\vec{q})$ is said to be a global PNE if for all $\vec{a} \in \vec{\mathcal{A}}$ and all $\vec{q} \in \vec{\mathcal{Q}}$:

$$\vec{P}(\vec{A}^*, \vec{A}^*(\vec{q}), \vec{q}) \geq P(\vec{A}^*, \vec{a}, \vec{q})$$

C.4 A General Theorem on Single Crossing Games

The following theorem is first presented for the situation in which the game has only one rôle. This is extended to n-rôles in Proposition C.5. Rôle indices have been dropped for notational convenience.

Proposition C.2 *Suppose that $\mathcal{Q}$ and $\mathcal{A}$ are compact subsets of the extended real numbers. Assume that $P(A, a, q)$ is continuous in A under the integral norm:*

$$\| A \| = \int_{\mathcal{Q}} | A(q) | \cdot dq$$

for all $A \in \mathcal{I}$ and continuous in a for all $q \in \mathcal{Q}$ and $A \in \mathcal{I}$, where:

$$\mathcal{I} \overset{\text{def}}{=} \{A(q); A(q) \text{ non-decreasing, and } A(q) \subseteq \mathcal{A}, a.e.\} \subset L^1(\mathcal{Q})$$

and $L^1(\mathcal{Q})$ is the set of Lebesgue integrable functions on $\mathcal{Q}$. .Further assume that:

$$P(A, a_2, q_2) - P(A, a_1, q_2) > P(A, a_2, q_1) - P(A, a_1, q_1) \qquad \text{(C.6)}$$

whenever $a_2 > a_1$ and $q_2 > q_1$.

Under these conditions any PNE of the game defined by $P$with respect to $\mathcal{I}$, is increasing in q. Moreover, at least one such PNE exists.

Equation (C.6), may be written as:

$$P_{23}(A, a, q) > 0$$

provided P is 'differentiable enough'

Proof: The proof is broken into eleven sections which are labelled for internal reference and for reference in non-mathematical discussion of the proof. The first eight sections of the proof restrict attention to the case in which $\mathcal{A}$ is a compact connected set (i.e. a closed interval). The more general case of an arbitrary compact set is dealt with in the final three sections, (sections [9] through [11]).

The proof of the proposition will proceed as follows: Under the assumption that $\mathcal{A}$ is a closed interval, it is first shown that for any $A \in \mathcal{I}$ there exists a function A_R, unique up to a set of measure 0, which satisfies:

$$P(A, A_R(q), q) \geq P(A, a, q), \quad \text{for all } a \neq A_R(q) \qquad \text{(C.7)}$$

with the inequality strict for almost all q. This function is called the 'best response function', is bounded and will be shown to be increasing, hence it is Lebesgue measurable. After checking a few necessary conditions, an application of Schauder's Fixed Point Theorem will then give the existence of a PNE in the circumstance in which $\mathcal{A}$ is an interval. The result for general compact sets is obtained by extending P to the convex hull of $\mathcal{A}$, denoted by $\bar{\mathcal{A}}$, in a manner so that the PBR to any increasing function taking values in $\bar{\mathcal{A}}$ is an increasing function of $\mathcal{Q}$ taking values in $\mathcal{A}$. Thus by the first eight sections of the proof there exists a PNE to this extended P, and as all PBRs take values in $\mathcal{A}$ this PNE must lie within the general compact set $\mathcal{A}$.

Note that numerical subscripts in this proof do not refer to different rôles but are used to distinguish different values of the particular variable.

[1]: In this section, and sections [2] to [8], it is assumed that $\mathcal{A}$ is an interval $[a_{\min}, a_{\max}]$ with $a_{\max} - a_{\min} < \infty$. The proof contained here can be trivially extended to the case in which one or both of $a_{\max}$ and $a_{\min}$ are infinite by noting that such an interval is homeomorphic to $[0,1]$ (e.g. via an arctan transformation followed by a rescaling of the axis).

Let $A_r : \mathcal{Q} \to \mathcal{A}$ be the the relation which consists of all pairs (a_r, q_r) satisfying the inequality (C.7). As $\mathcal{A}$ is compact and P is continuous there is at least one a_r for each $q_r \in \mathcal{Q}$. Denote $\{(a', q'); (a', q') \in A_r \text{ and } q' = q\}$, by $A_r(q)$.

[2]: It is now shown that if $(a_2, q_2) \in A_r(q_2)$ and $(a_1, q_1) \in A_r(q_1)$ and $q_2 > q_1$ then $a_2 \geq a_1$. Trivially:

$$\begin{aligned} P(A, a_2, q_2) &\geq P(A, a_1, q_2) \\ P(A, a_1, q_1) &\geq P(A, a_2, q_1) \end{aligned}$$

which may be rearranged to give:

$$P(A, a_1, q_1) - P(A, a_2, q_1) \geq P(A, a_1, q_2) - P(A, a_2, q_2)$$

If $a_1 > a_2$ this contradicts equation (C.6).

[3]: Next consider the subset $\mathcal{R}$ of $\mathcal{Q}$ defined by:

$$\mathcal{R} \stackrel{\text{def}}{=} \{q; \mathrm{card}(A_r(q)) > 1\}$$

For each $q \in \mathcal{R}$ choose $a_q^+, a_q^- \in A_r(q)$ so that $a_q^+ > a_q^-$, and let:

$$\mathcal{R}_n \stackrel{\text{def}}{=} \{q; a_q^+ - a_q^- \geq 1/n\}$$

Each $\mathcal{R}_n$ has finite cardinality as [2] implies that $A_r(q_1) \cap (a_{q_2}^-, a_{q_2}^+) = \emptyset$ for all $q_1 \neq q_2 \in \mathcal{Q}$, and thus by a standard result (Hungerford 1974, p20):

$$\mathrm{card}(\mathcal{R}) \leq \mathrm{card}\left(\bigcup_{n=1}^{\infty} \mathcal{R}_n \right) \leq \aleph_0$$

Thus A_r is a function except on a countable set.

[4]: Let A_R be some choice function (Munkres 1975), that is a function:

$$A_R : \{\{A_r(q)\}; q \in \mathcal{Q}\} \to \bigcup_q \{A_r(q)\}$$

with $A_R(\{A_r(q)\}) \in \{A_r(q)\}$. Identifying the domain of A_R with $\mathcal{Q}$, [3] shows that any choice function differs on a set of measure 0 at most. The final stages of this proof requires the application of Schauder's fixed point theorem which requires that we work in the Banach space $\mathcal{L}^1(\mathcal{Q})$ which is obtained from $L^1(\mathcal{Q})$ by factoring out the subspace generated by the functions that differ from the function $f(q) = 0$ on a set of measure zero. (The norm being as defined in the statement of the proposition.) It should be noted that A_R is increasing by [2], and is thus measurable (e.g. Goffman 1953, p182) and is contained in $L^1(\mathcal{Q})$ as it is bounded. Thus, the restrictions of all possible A_R to $\mathcal{L}^1(\mathcal{Q})$ exist and are identical.

[5]: Recall Schauder's Fixed Point Theorem (Deimling 1985 (Theorem 8.8) or Saaty & Bram 1964 (p372)):

> Theorem: Let $\mathcal{X}$ be a real Banach Space, $\mathcal{S} \subset \mathcal{X}$ non-empty, closed, bounded and convex, $M : \mathcal{S} \to \mathcal{S}$ be compact and continuous, then M has a fixed point.

Let $\mathcal{S}$ be the image of $\mathcal{I}$ in $\mathcal{L}^1(\mathcal{Q})$ after the quotient projection. $\mathcal{S}$ is non-empty, convex and compact (hence closed and bounded) by Lemma 4 of (Grafen 1990a). Identify $M(A)$ with the equivalence class of A_R. This is well defined as the payoff function is continuous in A. M is compact as it maps $\mathcal{S}$ onto $\mathcal{S}$.

All that is left to show is the continuity of the functional $M : \mathcal{S} \to \mathcal{S}$ defined by $M(A) = A_R$. If this can be shown to be the case, then $M(A)$ has a fixed point which, by the definition of M, is a PNE.

[6]: First it needs to be shown that:

$$P^\circ(A_1, A_2(q), q) \overset{\text{def}}{=} P(A_1, A_2(q), q) - P(A_1, a_{\min}, q)$$

is integrable for all A_1 and $A_2 \in \mathcal{I}$. This result will be obtained by an application of the Lebesgue Dominated Convergence Theorem (Fleming 1977, p232). The result is required to show that a certain function used in part [7] of the proof is well defined.

Suppose A_1 and $A_2 \in \mathcal{I}$. Increasing functions have at most a countable number of discontinuities. Thus, as $P^\circ(A_1, a, q)$ is continuous in a, $P^\circ(A_1, A_2(q'), q)$ has at most a countable number of discontinuities with respect to q' Moreover, as $\mathcal{A}$ is compact and $P^\circ(A_1, a, q)$ is continuous in a, it is also bounded, for each A_1 and q. This implies that $P^\circ(A_1, A_2(q'), q)$ is Riemann integrable in q' (Sprecher 1970, p297), and hence Lebesgue integrable (Sprecher 1970, p301)

Next consider the chain of successively finer partitions, $\mathcal{Q}^n$, of $\mathcal{Q}$ into 2^n intervals of equal length. For example:

$$\mathcal{Q}^2 = \left\{ \begin{array}{cc} \left[q_{\min}, \frac{q_{\max}-q_{\min}}{4}\right) & \left[\frac{q_{\max}-q_{\min}}{4}, \frac{q_{\max}-q_{\min}}{2}\right) \\ \left[\frac{q_{\max}-q_{\min}}{2}, \frac{3(q_{\max}-q_{\min})}{4}\right) & \left[\frac{3(q_{\max}-q_{\min})}{4}, q_{\max}\right] \end{array} \right\}$$

Denote the greatest lower bound of the ith element of $\mathcal{Q}^n$ in the natural ordering by q_i^n For example:

$$q_3^2 = \frac{q_{\max} - q_{\min}}{2}$$

Associate with each $\mathcal{Q}^n$ a function $P^\circ_{(n)}$ given by:

$$P^\circ_{(n)}(A_1, A_2, q) = P^\circ(A_1, A_2(q), q_i^n), \quad \text{wherever } q_i^n \leq q < q_{i+1}^n$$

Thus $P^\circ_{(n)}$ consists of n components of equal width, each of which is Lebesque integrable with respect to q. Therefore $P^\circ_{(n)}(A_1, A_2, q)$ is Lebesgue integrable with respect to q.

Set :

$$\begin{aligned} P^+(A, a, q) &\overset{\text{def}}{=} \max\{P^\circ(A, a, q_{\max}), 0\} \\ P^-(A, a, q) &\overset{\text{def}}{=} \max\{-P^\circ(A, a, q_{\min}), 0\} \end{aligned}$$

By equation (C.6) $\mid P^\circ_{(n)}(A_1, A_2, q) \mid$ is bounded above by:

$$P^+(A_1, A_2(q), q) + P^-(A_1, A_2(q), q) \tag{C.8}$$

for all n. Moreover, equation (C.8) is integrable as it is bounded and has at most a countable number of discontinuities.

Next consider, $\lim_{n\to\infty} P^{\circ}_{(n)}(A_1, A_2, q)$. $P^{\circ}(A_1, a, q)$ is increasing in q. This implies that the left and right limits of $P^{\circ}(A_1, a, q)$ with respect to q exist for all Q. Define:

$$p(q') \overset{\text{def}}{=} P^{\circ}(A_1, A_2(q'), q') - \lim_{q\uparrow q'} P^{\circ}(A_1, A_2(q'), q)$$

As $P^{\circ}(A, a, q)$ is increasing in q, it may be concluded that $p(q')$ is non-negative.

Define:

$$\begin{aligned} \mathcal{P} &\overset{\text{def}}{=} \{q; p(q) > 0\} \\ \mathcal{P}_m &\overset{\text{def}}{=} \{q; p(q) > 1/m\} \end{aligned}$$

By equation (C 6):

$$P^{\circ}(A_1, A_2(q'), q') \geq P^{\circ}(A_1, A_2(q'), q) + p(q'), \quad \text{for all } q < q'$$

Noting that equation (C.6), this implies that for all $a > A_2(q')$:

$$P^{\circ}(A_1, a, q') > P^{\circ}(A_1, a, q) + p(q'), \quad \text{for all } q < q'$$

Clearly $P^{\circ}(A_1, A_2(q_{\max}), q_{\max}) - P^{\circ}(A_1, A_2(q_{\max}), q_{\min}) \overset{\text{def}}{=} b$ is bounded and positive, and thus, by the previous equation it may be concluded:

$$\text{card}(\mathcal{P}) \leq \sum_{m=i}^{\infty} \text{card}(\mathcal{P}_m) \leq \sum_{m=i}^{\infty} b \cdot m \leq \aleph_0$$

Repeating this argument for limits from the right, shows that $P^{\circ}(A_1, a, q)$ is continuous in q at $a = A_2(q)$ except for at most a countable number of $q \in Q$. In turn this implies that $P^{\circ}_{(n)}(A_1, A_2, q)$ converges to $P^{\circ}(A_1, A_2(q), q)$ except for at most a countable number of $q \in Q$.

Lebesgue's Dominated Convergence Theorem (Fleming 1977, p232) then implies that $P^{\circ}(A_1, A_2(q), q)$ is Lebesgue integrable.

[7]: Any function that differs from A_R in $\mathcal{S}$, say $A_{R'}$ must have a lower global payoff than A_R. To see this, first note that the function $(P(A, A_R(q), q) - P(A, A_{R'}(q), q))$ is measurable as it is the sum of measurable functions (from [6] above). As this function is equal to its modulus and it is positive on a set of positive measure we have that:

$$\int_Q P(A, A_R(q), q) - P(A, A_{R'}(q), q) \cdot dq > 0,$$

by (Goffman 1953, p213) and thus the equivalence class of the pointwise best response A_R is also the unique global best response.

[8]: Lemma 2.8 can now be used to show that M is continuous. Identify both $\mathcal{U}$ and $\mathcal{V}$ with $\mathcal{S}$. Identify the $P(A, B)$ of Lemma 2.8 with:

$$\int_Q P(A, B(q), q) - P(A, a_{\min}, q) \cdot dq$$

Note that $P(A, B)$ is continuous in both its variables. By [7], M satisfies the uniqueness condition required by Lemma 2.8. Thus, M is continuous.

The conditions of Schauder's Fixed Point Theorem have been satisfied, so it may be concluded that there exists at least one $A^*(q)$ which is a PBR to itself. Therefore, A^* is a PNE.

[9]: We now turn to the general problem in which $\mathcal{A}$ is an arbitrary compact set. First it will be useful to characterise compact subsets of the real numbers. Consider an arbitrary point, a, in the convex hull of $\mathcal{A}$ (denoted $\bar{\mathcal{A}}$). Either a is in $\mathcal{A}$ or there exists $a_{\text{inf}} \in \mathcal{A}$ and $a_{\text{sup}} \in \mathcal{A}$ such that $a_{\text{inf}} \in \mathcal{A}$ and $(a_{\text{inf}}, a_{\text{sup}}) \cap \mathcal{A} = \emptyset$. To see this, suppose that $a \notin \mathcal{A}$ and no such a_{inf} existed. In this case a would be a limit point of $\mathcal{A}$, but as $\mathcal{A}$ is compact it contains all its limit point (Munkres 1975, p178) which contradicts the assumption that $a \notin \mathcal{A}$. A similar contradiction may be arrived at if it is assumed that a_{sup} does not exist. Thus $\mathcal{A}$ is a closed interval with open intervals excised (at most a countable number).

For each $A \in \mathcal{I}$ and each $a \in \bar{\mathcal{A}} - \mathcal{A}$ set:

$$P(A, a, q) \stackrel{\text{def}}{=} P(A, a_{\text{inf}}, q) + \frac{a - a_{\text{inf}}}{a_{\text{sup}} - a_{\text{inf}}} (P(A, a_{\text{sup}}, q) - P(A, a_{\text{inf}}, q)) \qquad (C.9)$$

Clearly, this new P satisfies the continuity conditions on a and A. Moreover, as:

$$P(A, a_{\text{sup}}, q_2) - P(A, a_{\text{inf}}, q_2) > P(A, a_{\text{sup}}, q_1) - P(A, a_{\text{inf}}, q_1)$$

whenever $q_2 > q_1$, this extension of P satisfies equation (C.6).

[10]: We need to continuously extend $P(A, a, q)$ to all $A \in \bar{\mathcal{I}}$ where:

$$\bar{\mathcal{I}} = \{A(q); A(q) \text{ non-decreasing, and } A(q) \subseteq \bar{\mathcal{A}}, \text{a.e.}\} \subset L^1(Q)$$

Such an extension is trivial as $\mathcal{I}$ is a retract (see Munkres 1975, p216 for definition) of $\bar{\mathcal{I}}$; one just need define $P(A, a, q)$ to be $P(r(A), a, q)$ where r is the retraction. To see that $\mathcal{I}$ is a retract of $\bar{\mathcal{I}}$ consider the mapping, $r : \bar{\mathcal{I}} \to \mathcal{I}$, defined in the following way. If $A(q) \in \mathcal{A}$ set $r(A)(q) = A(q)$. Given the above discussion on the nature of $\mathcal{A}$, as A is an increasing function the set of q for which $A(q) \notin \mathcal{A}$ is, at worst, the countable union of intervals. Suppose $A(q') \notin \mathcal{A}$. Define:

$$\begin{aligned} q_{\text{min}} &\stackrel{\text{def}}{=} \sup\{q; A(q) \in \mathcal{A} \text{ and } q < q'\} \\ q_{\text{max}} &\stackrel{\text{def}}{=} \inf\{q; A(q) \in \mathcal{A} \text{ and } q > q'\} \end{aligned}$$

Let a_{inf} and a_{sup} be as defined in [9] for $A(q')$, and set:

$$u(q') \stackrel{\text{def}}{=} \int_{q_{\text{min}}}^{q_{\text{max}}} (A(q) - a_{\text{inf}}) \cdot dq$$

Define:

$$r(A)(q') = \begin{cases} a_{\text{inf}} & \text{if } u(q') > (q' - q_{\text{min}})(a_{\text{sup}} - a_{\text{inf}}) \\ a_{\text{sup}} & \text{if } u(q') \leq (q' - q_{\text{min}})(a_{\text{sup}} - a_{\text{inf}}) \end{cases}$$

See Fig. 7 for an illustration of this defininition. Clearly, r is continuous in A under the integral norm as the distance between two functions in $\bar{\mathcal{I}}$, say A_1 and A_2, is greater than or equal to the distance between $r(A_1)$ and $r(A_2)$. As r maps $\bar{\mathcal{I}}$ onto $\mathcal{I}$, it is thus a retract. The payoff function, P, has now been extended to the convex hull of $\mathcal{A}$, which means that the results of parts [1] to [8] can be applied to show the existence of a PNE in $\bar{\mathcal{I}}$.

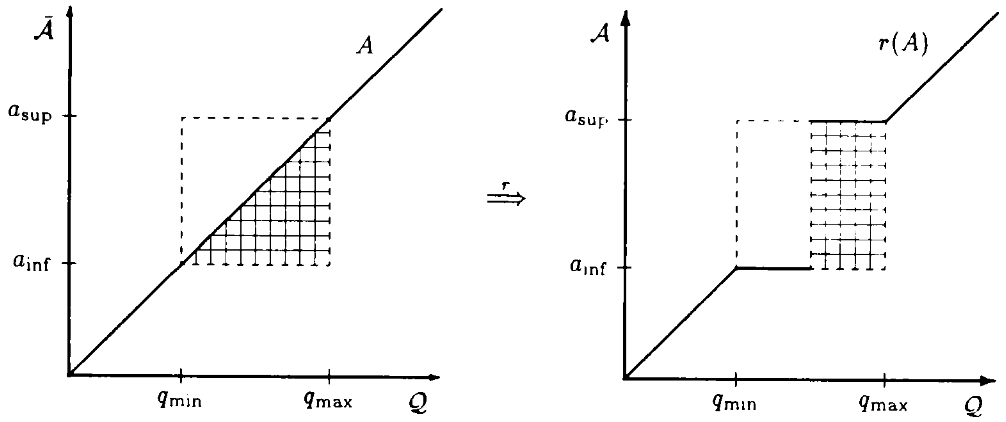

Figure 7: *Pictorial representation of the retract r. Portions of increasing functions, A, which lie outside of $\mathcal{A}$ are projected onto the closest boundary elements of $\mathcal{A}$ in such a way that the integral of A is unaffected over the range $[q_{\text{min}}, q_{\text{max}}]$, as can be seen by comparing the hatched areas above. Functions that are 'close' in $\bar{\mathcal{I}}$ with respect to the integral norm, will also be 'close' after being projected into $\mathcal{I}$.*

[11]: All that is left to be shown is that the PNE, which was shown to exist in [10], is contained in $\mathcal{I}$. Recall how P was extended to the convex hull of $\mathcal{A}$ in [9] by drawing lines between the boundary points of the open 'gaps' in $\mathcal{A}$ (equation (C.9)). A best response to A for a given q can only lie in $\bar{\mathcal{A}} - \mathcal{A}$ if P is constant over a gap in $\mathcal{A}$, as if the extension over all 'gaps' in $\mathcal{A}$ for a given q are of either positive or negative slope the PBR to A for a given q must lie in $\mathcal{A}$ because for each 'gap' one of $P(A, a_{\text{inf}}, q)$ or $P(A, a_{\text{sup}}, q)$ will be larger than the values taken by P on the 'gap' By equation (C.6), for each 'gap' there can exist at most one $q \in Q$ for which the extension over the 'gap' has zero slope.

By a covering argument similar to those used in [3] and [6] it is clear that there are a countable number of 'gaps' in $\mathcal{A}$ which implies that the PBR, A_R, to each $A \in \bar{\mathcal{I}}$ must lie in $\mathcal{I}$ except for a countable number of points. The value of $A_R(q)$ may be chosen to be an end point of the relevant 'gap' at the indeterminate points as the set of indeterminate q is of measure zero. As every PBR is contained in $\mathcal{I}$, every PNE is contained in $\mathcal{I}$. □

The philosophy behind the above proof is very simple: every continuous function from a compact space to a linearly ordered space obtains its maximum on that space. Therefore, as long as P is continuous we can then define a 'best response' to a given strategy. That is, no matter what the population signalling strategy is, as long as P is continuous, there will always exist at least one best response. Any strategy that is its own best response is a Nash equilibrium (PNE) and, as is shown in the next corollary, if it is a unique best response it must be an ESS.

Corollary C.3 *Assume the conditions of Proposition C.2. If A^* is a PNE of P then it is also an SNE. Conversely, if $F(A, q)$ is strictly increasing, then every SNE contains a PNE. If $F(A, q)$ is absolutely continuous and strictly increasing, then every SNE is an ESS.*

Proof: The first claim of the corollary follow trivially from part [6] of the proof of Proposition C.2.

The second claim is also trivial. The condition that $F(A,q)$ is strictly increasing is required to guarantee that there are no subsets of Q of positive measure on which $f(A,q)$ equals zero. If such a subset were to exist then a SNE, A^*, could be chosen to be arbitrary on it.

The final claim, that every SNE is an ESS, requires absolute continuity in $F(A,q)$. All that need be shown is that every SNE, A^*, is its unique best response under the integral norm defined by:

$$\| A - B \|_{A^*} = \int_Q \mid A(q) - B(q) \mid f(A^*,q) \cdot dq$$

Discontinuity in $F(A,q)$ at q' represents the circumstance in which there is a non-zero probability that a randomly selected individual in the population is of type q precisely. In other words, $f(A,q')$ is a multiple of a delta function. From part [3] of the proof of Proposition C.2 it can be seen that there is the possibility that any given q has more than one pointwise best response. If the SNE under consideration, A^*, contains more than one PNE, as would be the case if $\text{card}(A_r^*(q') {>} 1$ for some $q' \in Q$, and this q' coincided with a discontinuity in $F(A^*,q')$ then there can be no ESS. To see this, set a_1 and a_2 to be two distinct elements of $A_r^*(q')$ and:

$$A_i^*(q) = \begin{cases} A^*(q), & q \neq q' \\ a_i, & q = q' \end{cases}$$

Clearly, $\| A_1^* - A_2^* \|_{A^*} > 0$, but both are best responses to A^*.

If $F(A^*,q)$ is strictly increasing and continuous in q, then the integral defining the norm is just a standard Lebesgue integral, and as $f(A^*,q)$ is positive for almost all q, and there are no delta functions to worry about, is trivial to observe.

$$\| A - B \|_{A^*} = 0 \Longleftrightarrow \| A - B \| = 0$$

Part [6] of the proof of Proposition C.2 then shows that the best response to A^* is unique in $\mathcal{S}$. □

If P is smooth enough, then we have the following corollary

Corollary C.4 *Assume the conditions of Proposition C.2. If $P_{23}(A,a,q)$ exists and is greater tha zero for all $A \in \mathcal{I}$, $a \in \mathcal{A}$ and $q \in Q$, and $P_2(A,a,q)$ is continuous in a for all $A \in \mathcal{I}$ and $q \in Q$ then every ESS is strictly increasing except for possible initial and final intervals on which $A^*(q)$ equals $a_{\min}$ or $a_{\max}$ respectively.*

Proof: This results follows from the proof of Proposition C.2 upon noting that if $a' \in A_r(q')$ and $a' \neq a_{\max}$ or $a_{\min}$, then a' must be an internal maximum of $P(A,a,q')$ with respect to a. As P_2 is continuous this implies that $P_2(A,a',q') = 0$. Clearly $P_{23} > 0$ then implies that $P_2(A,a',q) > 0$ for all $q > q'$ from which it may be concluded that if $a' \in (a_{\min}, a_{\max})$ then it is in $A_r(q)$ for at most one q. □

C.5 Extension of Proposition C.2 to n-Rôles

Proposition C.5 *Suppose that* $\mathcal{Q}^{[i]}$ *and* $\mathcal{A}^{[i]}$ *are compact subsets of the extended real numbers. Assume that* $\vec{P}(\vec{A}, \vec{a}, \vec{q})$ *is continuous in* $\vec{A}$ *under the integral norm:*

$$\| \vec{A} \| = \sum_{i=1}^{n} \int_Q | A^{[i]}(q) | \cdot dq$$

for all $\vec{A} \in \vec{\mathcal{I}}$ *and continuous in* $\vec{a}$ *for all* $\vec{q} \in \vec{\mathcal{Q}}$ *and* $\vec{A} \in \vec{\mathcal{I}}$, *where.*

$$\vec{\mathcal{I}} \overset{def}{=} \{\vec{A}(\vec{q}); A^{[i]}(q^{[i]}) \text{ non-decreasing, and } A^{[i]}(q^{[i]}) \subseteq \mathcal{A}^{[i]}, a.e.\} \subset L^1(\mathcal{Q}^{[i]})$$

Further assume that:

$$P^{[i]}(\vec{A}, a_2^{[i]}, q_2^{[i]}) - P^{[i]}(\vec{A}, a_1^{[i]}, q_2^{[i]}) > P^{[i]}(\vec{A}, a_2^{[i]}, q_1^{[i]}) - P^{[i]}(\vec{A}, a_1^{[i]}, q_1^{[i]}) \quad \text{(C.10)}$$

for all i *whenever* $a_2^{[i]} > a_1^{[i]}$ *and* $q_2^{[i]} > q_1^{[i]}$

Under these conditions any PNE of the game defined by $\vec{P}$ *with respect to* $\vec{\mathcal{I}}$, *is increasing in* q. *Moreover, at least one such PNE exists.*

Proof: The result follow by an obvious extension of the proof of Proposition C.2. □

C.6 Allowable Transformations

Suppose that P defines a game that satisfies the conditions of Proposition C.2. The proof of Proposition C.2 shows that any ESS contains a PNE (Recall that as strategies that differ on a set of measure zero have the same payoff, ESSs must be viewed either as an equivalence class of functions which differ on a set of measure zero, or as elements of a factor space of the set of Lebesgue integrable functions arising from factoring out functions that differ from zero on a set of measure zero.) Any transformation of P which leaves the ordering of $P(A, a, q)$ with respect to a unchanged for each $A \in \mathcal{I}$ a $q \in Q$ does not affect the the functional M and hence does not affect the set of PBRs, the set of PNEs, and hence the set of ESSs. (Though if the transformation is nasty enough, there is the possibility that the integrated payoff may not be defined in the transformed problem. The best solution to this problem would seem to be to define the notion of ESS within the pre-transformed problem. My guess is that this will be independent of the particular pre- environment.)

The following is a non-exhaustive list of the kinds of transformation that may be applied to P without affecting the set of ESSs. They may be applied more than once and in any order. That is, the composition of allowable transformations is an allowable transformation:

1. Additon or subtraction of a function of A and q, i.e.

   $$P(A, a, q) \mapsto P(A, a, q) + T(A, q)$$

2. Multiplication by a function of A and q, i.e.

   $$P(A, a, q) \mapsto P(A, a, q)T(A, q)$$

   or equivalently, division by a non-zero function of A and q.

3. Any monotonically increasing transformation of P, e.g.

$$P(A,a,q) \mapsto \exp(P(A,a,q))$$

or $P(A,a,q) \mapsto P^n(A,a,q)$ where n is any odd positive integer. If P is positive then:

$$P(A,a,q) \mapsto \ln(P(A,a,q)$$

or $P(A,a,q) \mapsto P^n(A,a,q)$ where n is any positive number. It should be noted that two successive monotonically decreasing transformations are a monotincally increasing transformation, thus:

$$P(A,a,q) \mapsto \frac{-1}{P(A,a,q)}$$

is an allowable transformation.

The transformed payoff function need not satisfy the conditions of Proposition C.2. This is, of course, the importance of allowable transformations; they allow us to apply the results of Proposition C.2 to games defined by payoff functions which do not satisfy the conditions of Proposition C.2. If P does not satisfy the conditions of Proposition C.2, but there exists a transformation, T whose inverse is an allowable transformation for which $T(P)$ does satisfy the conditions of Proposition C.2, then we may apply Proposition C.2 to $T(P)$ and hence to $T^{-1} \circ T(P) = P$

Invertible transformations of the underlying variables a and q may also be useful in extending the application of Proposition C.2.

C.7 Extending PNEs to Boundaries

In the next section I will show how Nash's classical existence result for games in normal form is a corollary of Proposition C.5. The fundamental difference between games in normal form and the games considered in Proposition C.5 is that in the former games all individuals in a particular rôle are considered to be identical. Thus, instead of the payoffs satisfying equation (C.10), in a standard game in normal form the payoffs satisfy the same equation with the inequality replaced by equality:

$$P^{[i]}(\vec{A}, a_2, q_2) - P(\vec{A}, a_1, q_2) = P(\vec{A}, a_2, q_1) - P(\vec{A}, a_1, q_1) \qquad \text{(C.11)}$$

for all i, $\vec{A}$, a_1, a_2, q_1, and q_2. In this case q should not be interpreted as 'quality', but as a labelling which is useful when dealing with mixed-strategies (see section C.8 below).

Consider a continuum of games $P_t(A,B)$ parameterized by $t \in [t_{\min}, t_{\max}]$

Lemma C.1 *Denote the set of SNEs to P_t by $\mathcal{S}_t$. Assume that $P_t(A,a,q)$ is continuous in t for all $(A,a,q,t) \in \mathcal{I} \times \mathcal{A} \times \mathcal{Q} \times [t_1,t_2]$. If for each $t \in (t_1,t_2]$ each P_t has at least one SNE, then P_{t_1} has at least one SNE.*

Proof: Consider $\Phi_t(A)$ as defined in the proof of Proposition 4.3. As $[t_1,t_2] \times \mathcal{I}$ is compact, $\Phi_t(A)$ is uniformly continuous in (t,A).

Consider the sequence $\{s_i\} \stackrel{\text{def}}{=} \{t_1 + \frac{t_2-t_1}{2^i}\}$. Associate with this sequence, a sequence $\{A_i\}$ satisfying $A_i \in \mathcal{S}_{s_i}$. As $\mathcal{I}$ is compact, $\{A_i\}$ has a limit point, $A_\infty \in \mathcal{I}$ (Munkres 1975, p178). Continuity of $\Phi_t(A)$ in (t, A) implies that $\Phi_{t_1}(A_\infty) = 0$.
□

C.8 The Existence of Nash Equilibria to Games in Normal Form

Before we can prove Nash's result, we need to translate normal form games into a notation compatible with that used here. A game in normal form consists of n-rôles each with m_i pure strategies, denoted $\{a_1^{[i]}, a_2^{[i]}, \ldots, a_{m_i}^{[i]}\} \stackrel{\text{def}}{=} \mathcal{A}^{[i]}$. Without loss of generality, we may assume that each of the $a_j^{[i]}$ is a real number and that $a_j^{[i]} < a_{j+1}^{[i]}$ for all i, j.

Set $\mathcal{Q}^{[i]} \stackrel{\text{def}}{=} [0,1]$ and denote the set of increasing functions from $\mathcal{Q}^{[i]}$ to $\mathcal{A}^{[i]}$ by $\mathcal{I}^{[i]}$. Such functions can be represented uniquely (up to a finite number of points) by m_i non-negative numbers, say $\{p_1^{[i]}, p_2^{[i]}, \ldots, p_{m_i}^{[i]}\}$ which satisfy $\sum_{j=1}^{m_i} p_j^{[i]} = 1$; $A^{[i]}(q^{[i]})$ then equals $a_j^{[i]}$ where j satisfies:

$$j = \min\{k; \sum_{\ell=1}^{k} p_\ell^{[i]} \geq q^{[i]}\}$$

Thus, each increasing function $A^{[i]}$ may be considered a unique represention of a mixed strategy for rôle i.

Denote the payoff to an individual in rôle i playing $a_{j_i}^{[i]}$ against $n-1$ opponents playing $a_{j_k}^{[k]}$ by $b^{[i]}(j_1, j_2, \ldots, j_n)$. Any game in normal form may then be represented by a payoff function $\vec{P}(\vec{A}, \vec{a}, \vec{q})$ which is given by:

$$P^{[i]}(\vec{A}, a_{j_i}^{[i]}, q^{[i]}) \stackrel{\text{def}}{=} \sum_{j_1=1}^{m_1} \cdots \sum_{j_{i-1}=1}^{m_{i-1}} \sum_{j_{i+1}=1}^{m_{i+1}} \cdots \sum_{j_n=1}^{m_n} \left(\frac{b^{[i]}(j_1, j_2, \ldots, j_n)}{p_{j_i}^{[i]}} \prod_{k=1}^{n} p_{j_k}^{[k]} \right)$$

Note that $\vec{P}$ is independent of $\vec{q}$, and thus $\vec{P}$ satisfies equation (C.11) and is continuous in $\vec{A}$.

Proposition C.6 *Let $\vec{P}$ be a payoff function to a game in normal form. Then there exists at least one SNE (i.e. Nash equilibrium) to the game defined by $\vec{P}$*

Proof: Consider the parameterized set of payoff functions $\vec{P}_\epsilon$ defined by:

$$P_\epsilon^{[i]}(\vec{A}, a_j^{[i]}, q^{[i]}) = P^{[i]}(\vec{A}, a_j^{[i]}, q^{[i]}) + j\epsilon q^{[i]}$$

Clearly $\vec{P}_\epsilon$ satisfies the conditions of Proposition C.5 for all $\epsilon > 0$. Thus $\vec{P}_\epsilon$ has at least one SNE for each $\epsilon > 0$. The result follows by an application of Lemma C.1
□

It is clear that Proposition C.5 may be used to derive a number of extensions to Nash's result (e.g. infinite strategy sets). The above proof may be applied to games in which some or all rôles are indistinguishable to the players or to games in which rôles are imperfectly known by appropriately weighted averaging of the payoffs.

D Program for Epistatic Handicap Model

```
' PROGRAM EPISTAT.BAS
' For modelling epistatic handicap process
' Skeleton version
' For MS-DOS QBASIC Interpreter

' Declare subroutines used in program
' Only code that may need to be changed quickly
' or which needs to be moved frequently during analysis
' has been made into subroutines

DECLARE SUB Statistics (H(), sp, st, sv)
DECLARE SUB Renormalize (H(), sp, st, sv)
DECLARE SUB InputData1 (sp, sv, st, Cp(), Cv(), Ct(), Mp(), Mv(), Mt(), n())
DECLARE SUB InitGeneFreq1 (Gj(), sp, st, sv)

' Setup Number of Alleles for: Preference, Trait, Viability
' Note that counting starts at 0, so sp=2 means 3 alleles
sp = 2: st = 2: sv = 1

' Setup Genetic Profile Matrices: Male, Female, Offspring,
' Spare Matrix for Working
' These matrices store gene frequencies in the obvious way
DIM Gm(sp, st, sv), Gf(sp, st, sv), Gj(sp, st, sv), Gk(sp, st, sv)

' Setup Costs of: Preference, Trait, Viability
' These matrices store chance of survival given genotype
DIM Cp(sp), Ct(st, sv), Cv(sv)

' Setup Mutation Matrices: Preference, Trait, Viability
' The matrices store chance per generation of mutation up
' or down one level for each loci
DIM Mp(1, sp), Mt(1, st), Mv(1, sv)

' Setup Assortative Mating Frequency Matrix
' Temporary storage of proportion of matings
' between each male and female genotype
DIM AM(sp, st)

' Setup Intensity of Preference
' Preference is pool comparison
' n is the number from which females choose
' Note that n=1 equates with random mating and
' 0<n<1 represents preference for males with traits less than average
DIM n(sp)

' Setup Trait Sum and Partial Trait Sum
' Ts(t) is the un-normalized proportion of males with trait t
' Tp(t) is the proportion of males with trait t or less
DIM Ts(st), Tp(-1 TO st)

' Generation Counter
G = 0

' Input Values of Trait Costs etc.
CALL InputData1(sp, sv, st, Cp(), Cv(), Ct(), Mp(), Mv(), Mt(), n())

' Setup Initial Allele Frequencies
CALL InitGeneFreq1(Gj(), sp, st, sv)

' Beginning of Main Program Loop

' Increase Generation
' Label 1 marks beginning of main program loop
1 G = G + 1


    ' Calculate Male and Female Allelic Frequencies after Preference,
    ' Trait and Viability Selection. Results not Normalized.

    FOR p = 0 TO sp
    FOR t = 0 TO st
    FOR v = 0 TO sv
        Gm(p, t, v) = Gj(p, t, v) * Ct(t, v) * Cv(v)
        Gf(p, t, v) = Gj(p, t, v) * Cp(p) * Cv(v)
    NEXT v, t, p
```

```
' Reset Offspring Allelic Frequency Matrix

FOR p = 0 TO sp
FOR t = 0 TO st
FOR v = 0 TO sv
        Gk(p, t, v) = 0: Gj(p, t, v) = 0
NEXT v, t, p


' Mating
' Calculate Frequencies of Pairings Between Types
' Preference is Pool Comparison
' Tt is the normalizing constant for males

        ' Reset Partial Trait Sums etc.

        Tt = 0
        FOR t = 0 TO st
                Ts(t) = 0: Tp(t) = 0
        NEXT t

        ' Calculate New Trait Sums

        FOR t = 0 TO st
        FOR p = 0 TO sp
        FOR v = 0 TO sv
                Ts(t) = Ts(t) + Gm(p, t, v)
                Tt = Tt + Gm(p, t, v)
        NEXT v, p, t

        ' Calculate New Partial Trait Sums

        FOR t = 0 TO st
                Tp(t) = Tp(t - 1) + Ts(t) / Tt
        NEXT t


        ' Calculate Assortative Mating Matrix

        FOR t = 0 TO st
        FOR p = 0 TO sp
                AM(p, t) = (Tp(t)) ^ n(p) - (Tp(t - 1)) ^ n(p)
        NEXT p, t


        ' Calculate New Offspring Allelic Frequencies Before Mutation
        ' Note that gg is added to eight different matrix elements as
        ' there are eight possible ways of inheriting genes at 3 loci
        ' from two haploid parents

        FOR pf = 0 TO sp
        FOR tf = 0 TO st
        FOR vf = 0 TO sv
        FOR pm = 0 TO sp
        FOR tm = 0 TO st
        FOR vm = 0 TO sv
                gg = Gf(pf, tf, vf) * AM(pf, tm) * Gm(pm, tm, vm) / Ts(tm)
                Gj(pf, tf, vf) = Gj(pf, tf, vf) + gg
                Gj(pf, tf, vm) = Gj(pf, tf, vm) + gg
                Gj(pf, tm, vf) = Gj(pf, tm, vf) + gg
                Gj(pf, tm, vm) = Gj(pf, tm, vm) + gg
                Gj(pm, tf, vf) = Gj(pm, tf, vf) + gg
                Gj(pm, tf, vm) = Gj(pm, tf, vm) + gg
                Gj(pm, tm, vf) = Gj(pm, tm, vf) + gg
                Gj(pm, tm, vm) = Gj(pm, tm, vm) + gg
        NEXT vm, tm, pm
        NEXT vf, tf, pf


' Mutation - Note that the results are unaffected by loci order

        ' Mutation in p - Note endpoint mutations calculated separately

        IF sp = 1 THEN 2
        FOR p = 1 TO (sp - 1)
        FOR t = 0 TO st
        FOR v = 0 TO sv
```

```
        Gk(p - 1, t, v) = Gk(p - 1, t, v) + Mp(0, p) * Gj(p, t, v)
        Gk(p + 1, t, v) = Gk(p + 1, t, v) + Mp(1, p) * Gj(p, t, v)
        Gk(p, t, v) = Gk(p, t, v) - Mp(1, p) * Gj(p, t, v) - Mp(0, p) * Gj(p, t, v)
NEXT v, t, p

2 'Mutation at endpoints

FOR t = 0 TO st
FOR v = 0 TO sv
        Gk(1, t, v) = Gk(1, t, v) + Mp(1, 0) * Gj(0, t, v)
        Gk(sp - 1, t, v) = Gk(sp - 1, t, v) + Mp(0, sp) * Gj(sp, t, v)
        Gk(0, t, v) = Gk(0, t, v) - Mp(1, 0) * Gj(0, t, v)
        Gk(sp, t, v) = Gk(sp, t, v) - Mp(0, sp) * Gj(sp, t, v)
NEXT v, t

' Make changes to zygotic genotype frequencies

FOR p = 0 TO sp
FOR t = 0 TO st
FOR v = 0 TO sv
        Gj(p, t, v) = Gj(p, t, v) + Gk(p, t, v)
        Gk(p, t, v) = 0
NEXT v, t, p


' Mutation in t - Note endpoint mutations calculated separately

IF st = 1 THEN 3
FOR t = 1 TO (st - 1)
FOR p = 0 TO sp
FOR v = 0 TO sv
        Gk(p, t - 1, v) = Gk(p, t - 1, v) + Mt(0, t) * Gj(p, t, v)
        Gk(p, t + 1, v) = Gk(p, t + 1, v) + Mt(1, t) * Gj(p, t, v)
        Gk(p, t, v) = Gk(p, t, v) - Mt(1, t) * Gj(p, t, v) - Mt(0, t) * Gj(p, t, v)
NEXT v, p, t

3 'Mutation at endpoints

FOR p = 0 TO sp
FOR v = 0 TO sv
        Gk(p, 1, v) = Gk(p, 1, v) + Mt(1, 0) * Gj(p, 0, v)
        Gk(p, st - 1, v) = Gk(p, st - 1, v) + Mt(0, st) * Gj(p, st, v)
        Gk(p, 0, v) = Gk(p, 0, v) - Mt(1, 0) * Gj(p, 0, v)
        Gk(p, st, v) = Gk(p, st, v) - Mt(0, st) * Gj(p, st, v)
NEXT v, p

' Make changes to zygotic genotype frequencies

FOR p = 0 TO sp
FOR t = 0 TO st
FOR v = 0 TO sv
        Gj(p, t, v) = Gj(p, t, v) + Gk(p, t, v)
        Gk(p, t, v) = 0
NEXT v, t, p


' Mutation in v - Note endpoint mutations calculated separately

IF sv = 1 THEN 4
FOR v = 1 TO (sv - 1)
FOR p = 0 TO sp
FOR t = 0 TO st
        Gk(p, t, v - 1) = Gk(p, t, v - 1) + Mv(0, v) * Gj(p, t, v)
        Gk(p, t, v + 1) = Gk(p, t, v + 1) + Mv(1, v) * Gj(p, t, v)
        Gk(p, t, v) = Gk(p, t, v) - Mv(1, v) * Gj(p, t, v) - Mv(0, v) * Gj(p, t, v)
NEXT t, p, v

4 'Mutation at endpoints

FOR p = 0 TO sp
FOR t = 0 TO st
        Gk(p, t, 1) = Gk(p, t, 1) + Mv(1, 0) * Gj(p, t, 0)
        Gk(p, t, sv - 1) = Gk(p, t, sv - 1) + Mv(0, sv) * Gj(p, t, sv)
        Gk(p, t, 0) = Gk(p, t, 0) - Mv(1, 0) * Gj(p, t, 0)
        Gk(p, t, sv) = Gk(p, t, sv) - Mv(0, sv) * Gj(p, t, sv)
NEXT t, p

' Make changes to zygotic genotype frequencies
```

```
                FOR p = 0 TO sp
                FOR t = 0 TO st
                FOR v = 0 TO sv
                        Gj(p, t, v) = Gj(p, t, v) + Gk(p, t, v)
                        Gk(p, t, v) = 0
                NEXT v, t, p


        ' Renormalize population so gene frequencies sum to 1

        CALL Renormalize(Gj(), sp, st, sv)


        ' Calculate and Print Statistics

        CALL Statistics(Gj(), sp, st, sv)


' Start next generation

GOTO 1

'END OF MAIN PROGRAM LOOP



' Data

' Cp
DATA 1,.6,.01

' Cv
DATA .7,1

' Ct
DATA 1,1,.8,.95,.1,.2

' Mp
DATA 0,.1,.1,.1,.1,0
' Mt
DATA 0,.1,.1, 1,.1,0

' Mv
DATA 0,0.05,.2,0

' n
DATA 1,2, 3



'Subroutines Called in Program

SUB InitGeneFreq1 (Gj(), sp, st, sv)

'Equal Gene Frequencies to Start

        s = (sp + 1) * (st + 1) * (sv + 1)
        FOR p = 0 TO sp
        FOR t = 0 TO st
        FOR v = 0 TO sv
              Gj(p, t, v) = 1 / s
        NEXT v, t, p

END SUB

SUB InputData1 (sp, sv, st, Cp(), Cv(), Ct(), Mp(), Mv(), Mt(), n())
' Read in Data

        ' Costs
        FOR p = 0 TO sp
                READ Cp(p)
        NEXT p
        FOR v = 0 TO sv
                READ Cv(v)
        NEXT v
        FOR t = 0 TO st
        FOR v = 0 TO sv
```

```
                READ Ct(t, v)
        NEXT v, t

        ' Mutation Matrixes
        FOR p = 0 TO sp
                READ Mp(0, p)
                READ Mp(1, p)
        NEXT p
        FOR t = 0 TO st
                READ Mt(0, t)
                READ Mt(1, t)
        NEXT t
        FOR v = 0 TO sv
                READ Mv(0, v)
                READ Mv(1, v)
        NEXT v

        ' Female Sample Sizes
        FOR p = 0 TO sp
                READ n(p)
        NEXT p

END SUB
SUB Renormalize (H(), sp, st, sv)

' Normalize Population

        d = 0
        FOR p = 0 TO sp
        FOR t = 0 TO st
        FOR v = 0 TO sv
                d = d + H(p, t, v)
        NEXT v, t, p
        FOR p = 0 TO sp
        FOR t = 0 TO st
        FOR v = 0 TO sv
                H(p, t, v) = H(p, t, v) / d
        NEXT v, t, p

END SUB

SUB Statistics (H(), sp, st, sv)

' Calculate Correlation Coefficients

        ' Set Statistics Equal Zero
        ' mux is mean of x
        ' vax is variance in x
        ' cxy is correlation between x and y
        mup = 0: mut = 0: muv = 0
        vap = 0: vat = 0: vav = 0
        cpt = 0: ctv = 0: cpv = 0

        ' Calculate Means
        FOR p = 0 TO sp
        FOR t = 0 TO st
        FOR v = 0 TO sv
                mup = mup + p * H(p, t, v)
                mut = mut + t * H(p, t, v)
                muv = muv + v * H(p, t, v)
        NEXT v, t, p

        ' Calculate Variances and Covariances
        FOR p = 0 TO sp
        FOR t = 0 TO st
        FOR v = 0 TO sv
                vap = vap + (p - mup) ^ 2 * H(p, t, v)
                vat = vat + (t - mut) ^ 2 * H(p, t, v)
                vav = vav + (v - muv) ^ 2 * H(p, t, v)
                cpt = cpt + (p - mup) * (t - mut) * H(p, t, v)
                ctv = ctv + (v - muv) * (t - mut) * H(p, t, v)
                cpv = cpv + (p - mup) * (v - muv) * H(p, t, v)
        NEXT v, t, p

        ' Calculate Correlation Coefficients
        rpt = cpt / SQR(vap) / SQR(vat)
        rtv = ctv / SQR(vav) / SQR(vat)
        rpv = cpv / SQR(vap) / SQR(vav)
```

```
    ' Print
    r = rpt * rtv
    PRINT "rpv"; rpv; "prod"; r
    PRINT "p"; mup; "t"; mut; "v"; muv

END SUB
```

IV

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