Optimality and Honesty

- Optimization
- Evolutionary game theory
- 2-person discrete contests
- Honesty vs deceit
- Read 364-371; 619-632, ch. 20

Optimality theory

- Tradeoffs in signal production and reception are common
  - e.g. louder calls carry farther but are more energetically costly to produce
- Optimization is the process of adjusting signal display to maximize benefits and minimize costs to sender and receiver
- May occur over evolutionary time for species or result from action of individual

Optimality terms

- Optimization criteria: rule used to identify best signaling strategy
  - Strategy = the behavioral response of an individual
  - Optimal strategy maximizes payoffs if freq. independent
- Payoff: value of alternative strategies
  - lifetime fitness
    - survival * fecundity
  - inclusive fitness
    - individual fitness of donor + (increase in fitness of relatives * relatedness of relatives to donor)
- Frequency independent: payoffs do not depend on others, only environment

When should communication occur?

- For sender
  - average PO(sender, signal) > average PO(sender, no signal)
- For receiver
  - average PO(receiver, signal) > average PO(receiver, no signal)
- The difference in payoffs with and without signal is the ‘average value of information’ in signal

Game theory

- Game theory is needed when the fitness consequences of a behavior depend on what others are doing, i.e. is frequency dependent
  - e.g. payoff for giving a distress call depends on frequency of individuals willing to help
- Economic vs evolutionary game theory
  - Economic games are zero-sum, i.e. increasing the payoff to one player decreases the payoff to others. Evolutionary games need not be zero-sum
  - Economic games use money as currency, evolutionary games use fitness

What is an ESS?

- Game solution is the best strategy
  - Social scientists require rational behavior
  - Evolution requires natural selection
  - A pair of strategies which represent the best replies to each alternative is a Nash equilibrium.
- ESS = a strategy which if adopted by all members of a population cannot be invaded by any alternative strategy
  - May lower population fitness

Game classification

- Strategy set
  - Discrete or continuous
- Role symmetry
  - Symmetric vs asymmetric
- Opponent number
  - 2-person contests vs n-person scrambles
- Sequential dependence
  - if outcomes of early decisions constrain later decisions, then the entire sequence is the game and each decision is a bout within the game. These are dynamic games.

2-person payoff matrix

		Opponent plays: Strategy 1	Opponent plays: Strategy 2
Focal player plays	Strategy 1	PO_{11}	PO_{12}
	Strategy 2	PO_{21}	PO_{22}

Figure 19.1 Payoff matrix for 2 × 2 discrete symmetric contest. Because the game is symmetric, the two players are interchangeable and we only need to list one payoff for each pair of strategies played. The convention is to list the playoffs to the player on the left. Payoffs are given in the same units for all cells in the matrix and denoted here by PO_{ij}. The first subscript (*i*) is the strategy played by the focal player and the second (*j*) is that of its opponent.

Evolution of display: Hawks & Doves

- Possible behaviors:
  - Display
  - Fight but risk injury
  - Retreat
- Possible strategies:
  - Hawk: fight until injured or opponent retreats
  - Dove: display initially but retreat if opponent attacks

Payoff matrix

Actor:	Opponent:	Hawk	Dove
	Hawk	(V-C)/2	V
	Dove	0	V/2

V = value of resource being contested

C = cost of fighting due to injury

Pure ESS

Resource > cost; V = 2; C = 1

Actor:	Opponent:	Hawk	Dove
	Hawk	● 1/2	● 2
	Dove	0	1

1/2 > 0, so Hawks resist invasion by doves
2 > 1, so Hawks can invade doves
ESS = all Hawks => pure ESS

Mixed ESS

Resource < cost; V = 1; C = 2

		Opponent: Hawk	Opponent: Dove
Actor:	Hawk	-1/2	● 1
	Dove	● 0	1/2

-1/2 < 0, so Doves can invade Hawks

1 > 1/2, so Hawks can invade doves

ESS = mix of Hawks and Doves =>
mixed stable ESS

Mixed ESS

Resource < cost; V = 1; C = 2

	Opponent:	Hawk	Dove
Actor:	Hawk	-1/2	● 1
	Dove	● 0	1/2

To calculate the frequency of each strategy at the ESS, you must 'discount' payoffs by the probability of occurrence

– the fitness consequence of each possible outcome * the probability that each outcome occurs

So, assume that the frequency of Hawks is p, and Doves is 1-p

at the ESS the fitness of Hawks must equal the fitness of Doves, then

$W_H = 1/2(V-C)p + V(1-p)$

$W_D = 1/2(1-p)$ which after substituting payoffs is

$(-1/2)p + (1-p) = (0)p + (1/2)(1-p)$; $1 - 3p/2 = 1/2 - p/2$

$1/2 = p$ (equal proportion of doves and hawks at the ESS)

2-person ESS alternatives

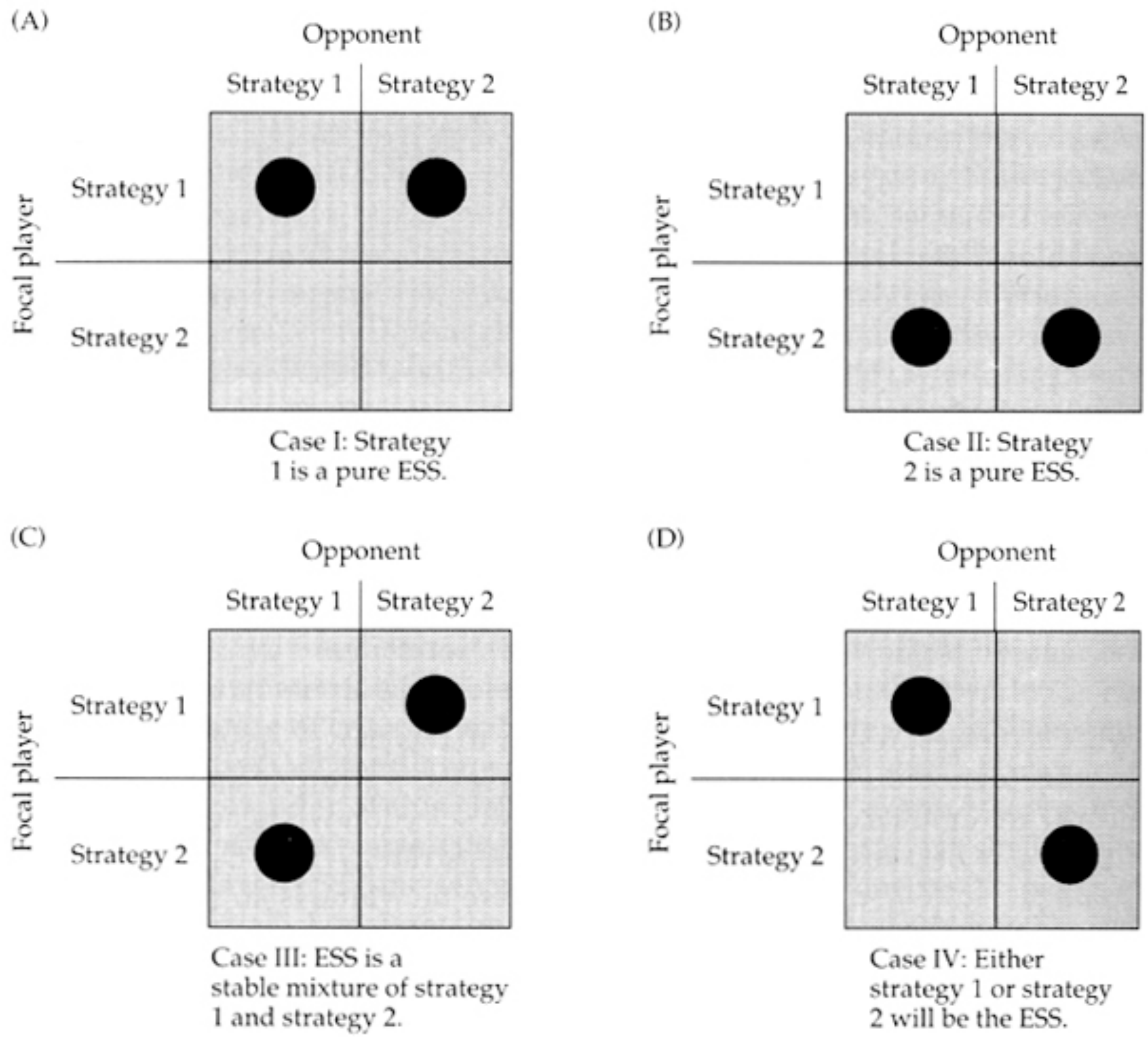
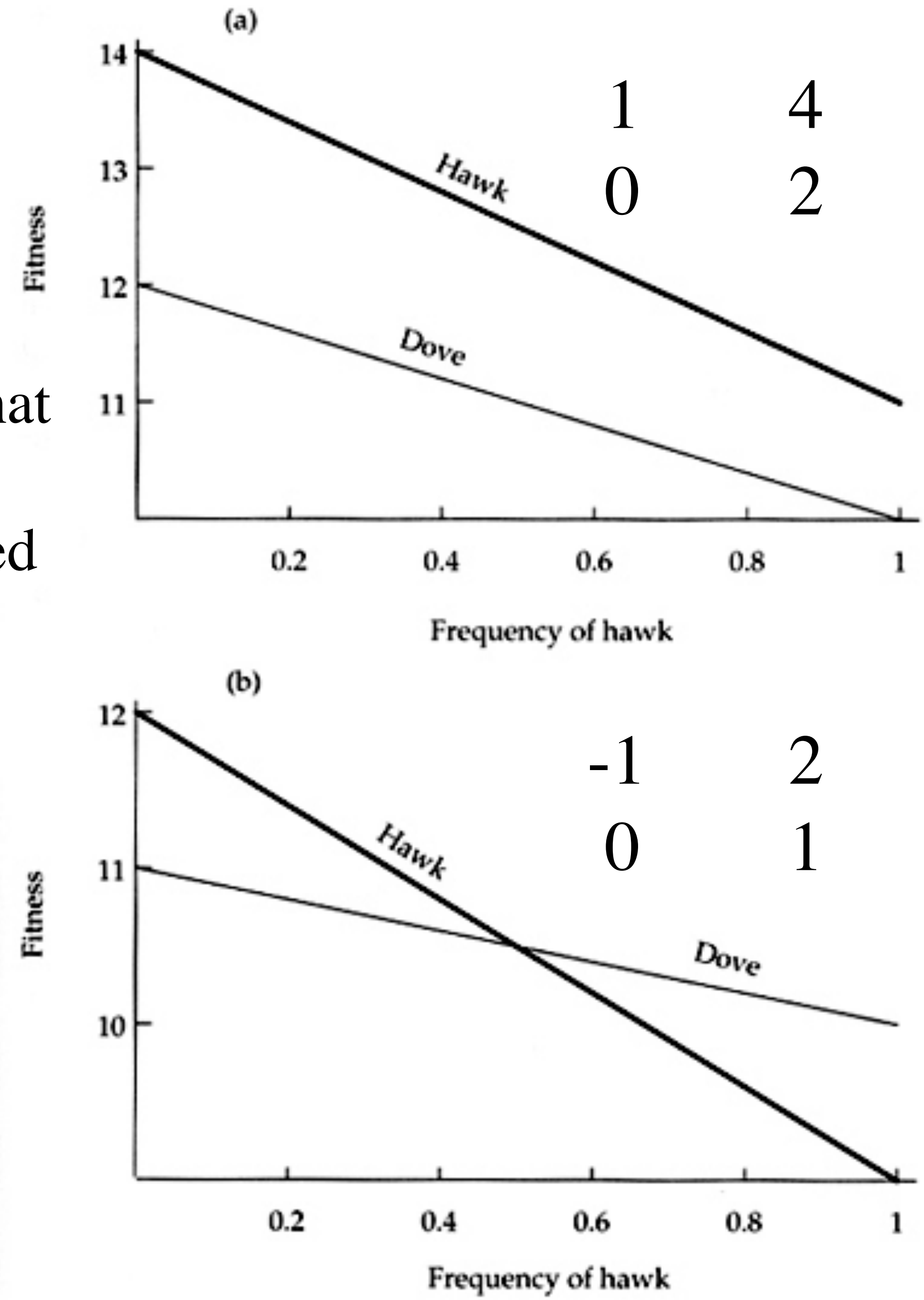


Figure 19.2 Possible ESSs in 2 × 2 discrete symmetric contest. For each column in the payoff matrix, a dot is placed in that cell conferring the best payoff to the focal

Frequency dependence

Frequency dependence means that fitness depends on strategy frequency. This can be illustrated by plotting fitness against freq.

$W_H = W_o + 1/2(V-C)p + V(1-p)$
$W_D = W_o + 1/2(1-p)$



Mixed ESS mechanisms

- Stable strategy set in which a single individual sometimes performs one strategy and sometimes another with probability p
- Stable polymorphic state in which a fraction, p, of the population adopts one strategy while the remainder, 1-p, adopts the other

Side-blotched lizards

Uta stansburiana

- Three throat color morphs, blue, orange & yellow
  - Blue males mate guard females against yellow males, but are ineffective against aggressive orange males
  - Orange males maintain large territories but are cuckolded by yellow males
  - Yellow males sneak copulations
- Throat color is determined by a 3 allele system and, therefore, appears to be a stable polymorphism

Zamudio & Sinervo 2000 PNAS 97:14427; Sinervo & Clobert 2003 Science 300:1949

Take Game Payoff Matrix

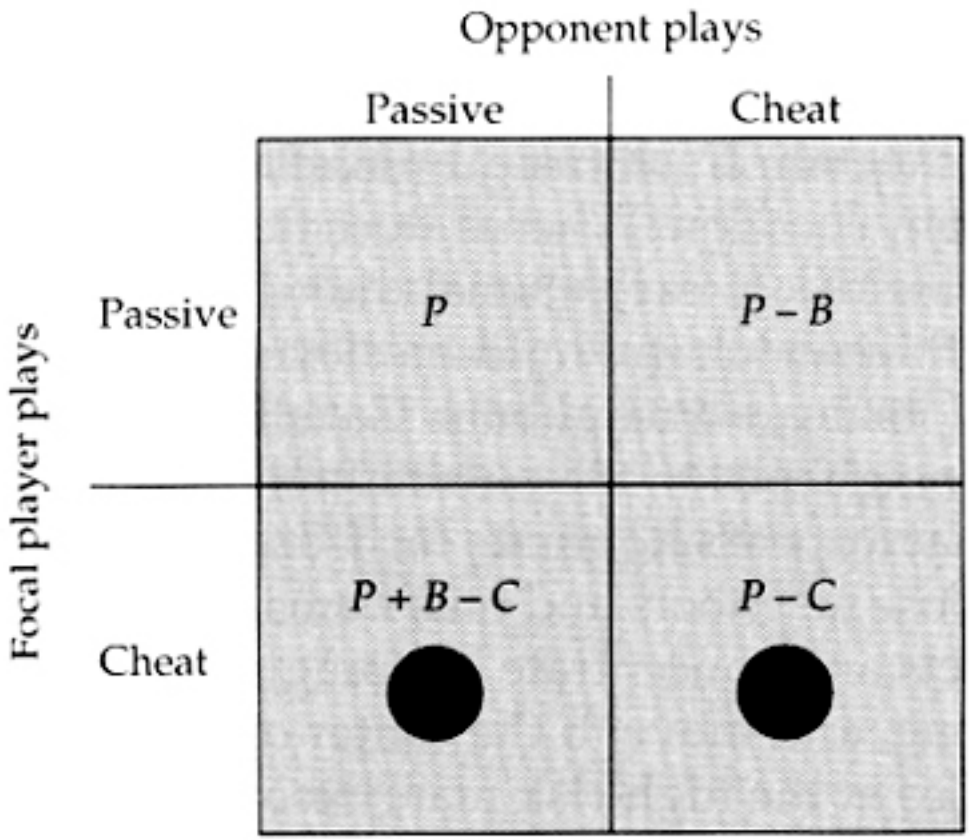


Figure 19.4 Payoff matrix for a take game. Passive animals mind their own business. *P* is the payoff when both players mind their own business. Cheats steal an average of *B* fitness units from other players at a cost to themselves of –*C* fitness units. Dot analysis indicates that cheat is a pure ESS as long as B > C.

Conclusion: if cheating pays, why be honest?

Honesty vs. cheating

- Sender deceives receiver
  - emits false signal
    - lie (false categorical signal)
    - bluff or exaggerate (continuous signal)
    - attenuator (makes assessment more difficult)
  - withholds signal, e.g. alarm or food location
- Receiver exploits sender

Signal honesty in perspective

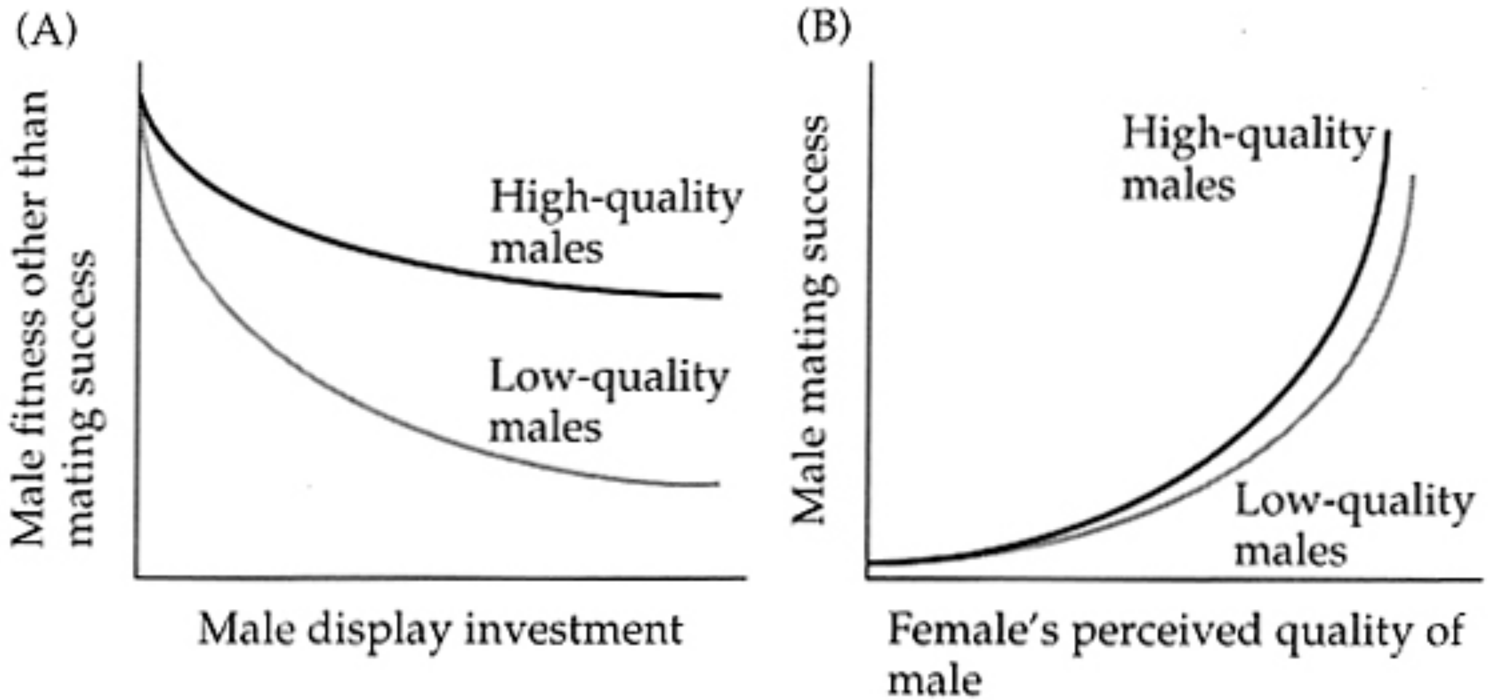
- Classic ethology (Lorenz, and others)
  - all signals are honest because source of signal is linked to motivation
- Game theory (Dawkins and Krebs 1978)
  - Arms race occurs between deceitful signalers and discriminating receivers
- Signals as handicaps (Zahavi 1977; Grafen 1990)
  - Receivers only attend to costly signals, which can only be produced by honest senders

Evolutionary games on honesty

Table 20.2 Summary of evolutionary games on honest signaling

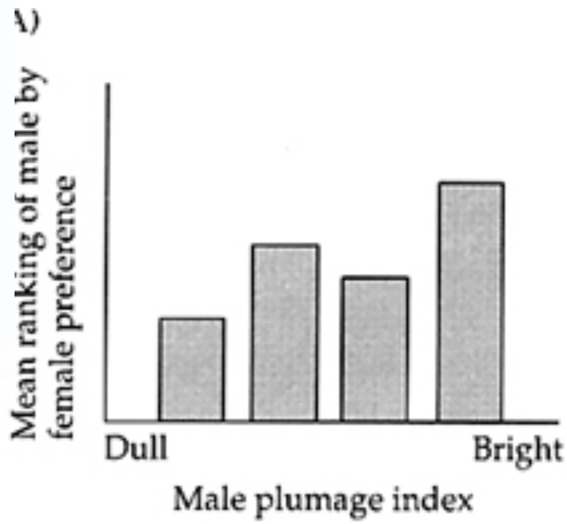
Function	Sender strategies	Game type	Honesty conditions	References
Agonistic contests	Select display according to effectiveness and cost to sender. Honest sender selects display indicating true motivation; selection of dishonest sender exaggerates true motivation.	Discrete asymmetric contest	Requires a positive correlation between display effectiveness and sender cost.	Enquist 1985; Enquist et al. 1985
Courtship	Display with intensity higher than competitors, to attract mates. Honest senders adjust intensity to match relative quality assayed by females; dishonest senders exaggerate by giving higher intensity than justified by quality.	Continuous asymmetric scramble	Display must be costly to senders, with greater costs at given intensity for lower-quality males.	Grafen 1990a,b
Badges of status	Display badge with size indicating dominance rank. Honest senders adjust badge size to reflect true status; dishonest senders sport badge with either too large or too small a size.	Continuous symmetric contest	Cost of escalated fights must increase with badge size, and large-badged animals must be challenged often by other large-badged animals.	Maynard Smith and Harper 1988
		Discrete symmetric contest	Same as above plus there must be a contest-independent cost of being aggressive.	Owens and Hartley 1991; Johnstone and Norris 1993
Begging (Sir Philip Sidney game)	Sender signals demand for help to receiver. Honest senders only signal when in need; dishonest senders always signal. Receiver benefits only indirectly from giving to sender.	Discrete asymmetric contest	Begging must be costly to senders.	Maynard Smith 1991
		Continuous asymmetric contest	Sender costs are highest when an intermediate level of relatedness between sender and receiver exists.	Godfray 1991; Johnstone and Grafen 1992
Amplifiers	Display trait facilitating accurate direct assessment of sender qualities. Honest sender sports amplifier; dishonest shows attenuator.	Genetic models	Amplifiers can evolve if average benefits to high-quality senders are greater than average costs to low-quality ones.	Hasson 1989b, 1990; Hasson et al. 1992; Michod and Hasson 1990
Predator notification	Prey display to predator that they are not worth chasing. Honest sender shows true agility or condition; dishonest sender uses noninformative display.	Continuous asymmetric contest	Display must be costly, with lower-quality senders paying higher cost for a given display level.	Vega-Redondo and Hasson 1993

Grafen's handicap signaling model



- Honest signaling evolves when
  - Signaling is costly to males
  - Costs to low quality males are higher than to high quality males
  - High quality males have higher probability of mating

House finches signal with carotenoids



Carotenoids cannot be synthesized, so their display by males provides an honest measure of a male's foraging ability

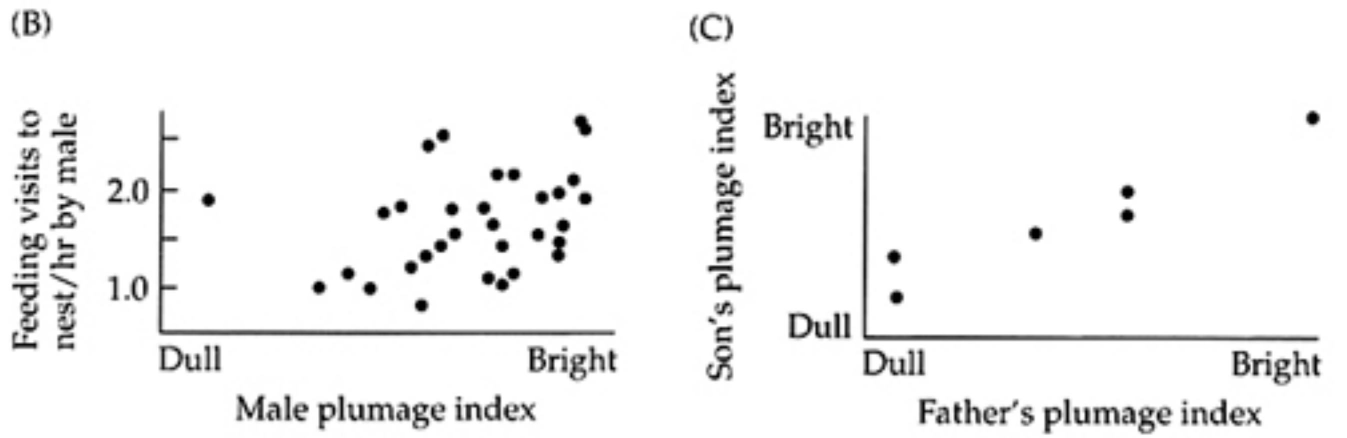


Figure 20.5 Female choice of mate and carotenoid colors of male house finches

Experimental verification of handicaps remains limited

THE ROYAL SOCIETY

Received 10 September 2003
Accepted 16 January 2004
Published online 16 March 2004

Review Paper

Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis?

Samuel Cotton[1], **Kevin Fowler**[1] **and Andrew Pomiankowski**[1,2*]

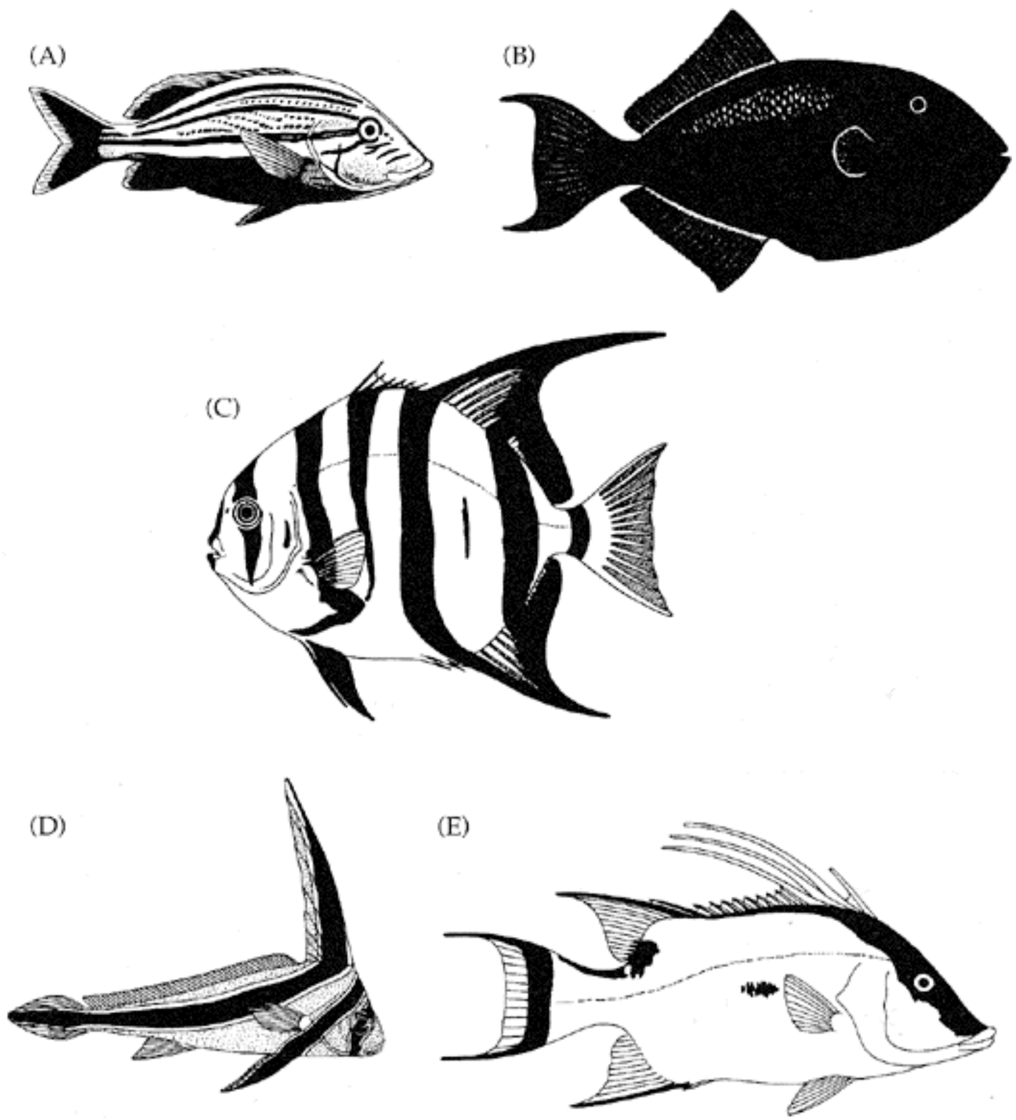
[1]*The Galton Laboratory, Department of Biology, University College London, 4 Stephenson Way, London NW1 2HE, UK*
[2]*Collegium Budapest, Szentháromság utca 2, H-1014 Budapest, Hungary*

The handicap hypothesis of sexual selection predicts that sexual ornaments have evolved heightened condition-dependent expression. The prediction has only recently been subject to experimental investigation. Many of the experiments are of limited value as they: (i) fail to compare condition dependence in sexual ornaments with suitable non-sexual trait controls; (ii) do not adequately account for body size variation; and (iii) typically consider no stress and extreme stress manipulations rather than a range of stresses similar to those experienced in nature. There is also a dearth of experimental studies investigating the genetic basis of condition dependence. Despite the common claim that sexual ornaments are condition-dependent, the unexpected conclusion from our literature review is that there is little support from well-designed experiments.

Yet deceit and exaggeration occurs

- Foraging birds give alarm calls to scare competitors away from food (Møller)
- Rhesus macaques will withhold food calls when food is discovered unless relatives are nearby (Hauser)
- Mantis shrimp will threaten after molting when vulnerable (Adams & Caldwell)
- Features may amplify or attenuate information

Amplifiers of fish body size



Amplifier: a trait that makes direct assessment or use of cues less costly or more accurate

Attenuator: a trait that makes direct or cue assessment more difficult.

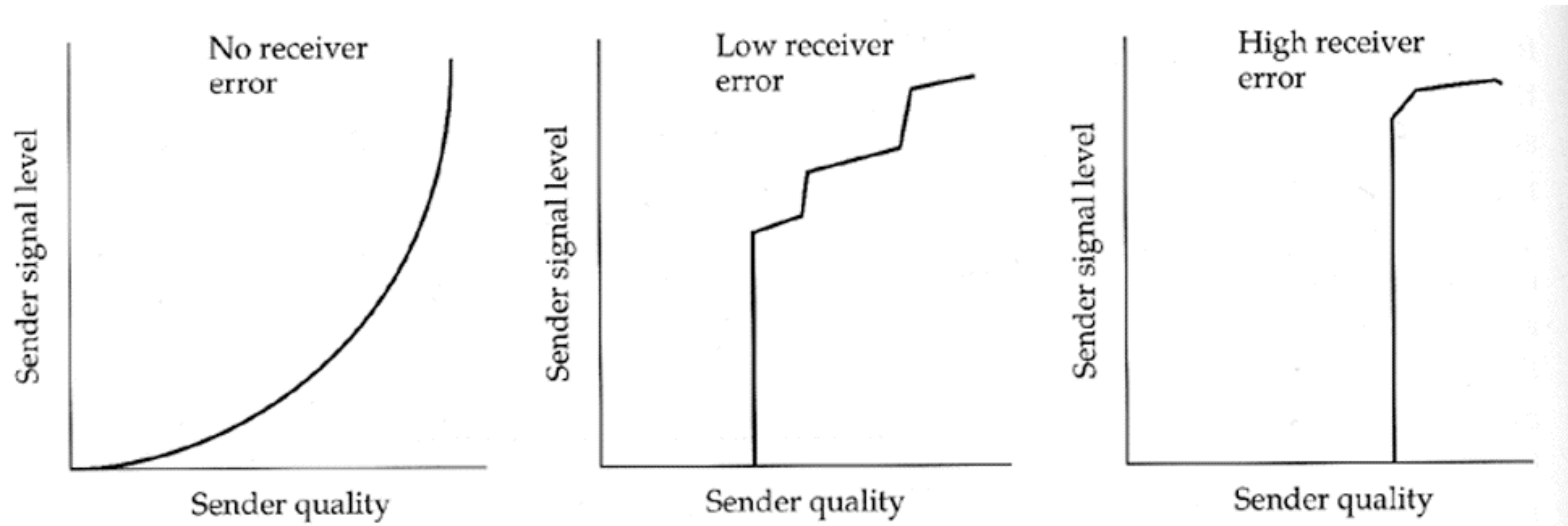
Why does deceit exist?

- Evolving signaling systems are not at the ESS
- Perceptual error by receivers allows cheaters to escape detection
- Receivers may have to deal with multiple types of senders- some honest and some cheaters

Consequences of receiver error

- Adding perceptual error to games insures that all strategies are tested and thereby improves stability
- Senders need not be perfectly honest
  - If receiver error is 10%, why should a male signal 10% more than another male?
  - Senders should increment displays in steps according to magnitude of error

Receiver error in handicap models



Low quality senders should only signal if it can be perceived

As error increases, potential for dishonesty also increases

High receiver error could be alternative explanation for stereotypy

Consequences of multiple senders

- What if there are two beggars: one honest and one that always begs regardless of need? (Philip Sidney game)
- ESS is for receivers to respond to begging as long as beggars are honest, either because they
  - are closely related to receivers or
  - pay a higher cost than constant beggars or
  - are sufficiently more common than cheaters
- Provides explanation for systems with low levels of cheating