Noise, Signal Detection, and the Evolution of Communication

R. Haven Wiley

Department of Biology

University of North Carolina

Chapel Hill, NC 27599-3280, USA

http://www.unc.edu/~rhwiley

International Ethological Conference, Halifax, 22 August 2007

Revised 28 August 2007

Recent work in my lab on
signal detection and the evolution of communication

Evolution of receiver performance

Wiley 1994, 2000, 2006

Detection and discrimination in noise

Wollerman 1999, Wollerman and Wiley 2002a,b

For pdf files . . .

http://www.unc.edu/~rhwiley/pdfs/index.html

Outline

history

- noise and errors -- pervasive
- receiver performance evolves
- signals evolve -- current view

news

- signalers evolve -- signal-detection view
- signal-detection equilibrium
- new view of the evolution of communication

see addendum (1) for what a signal is

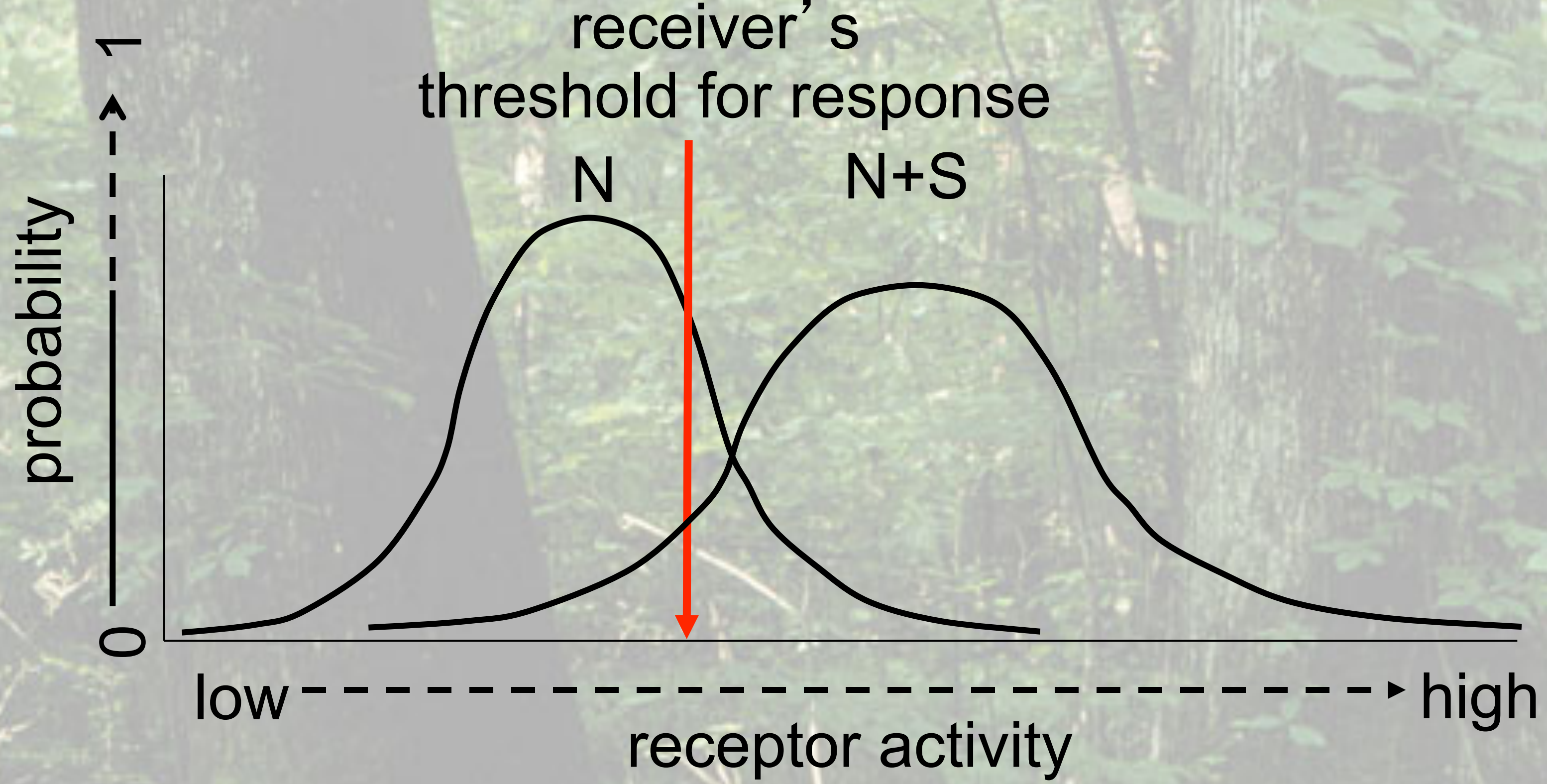
noise is pervasive

when signals come with noise (all real communication) . . .

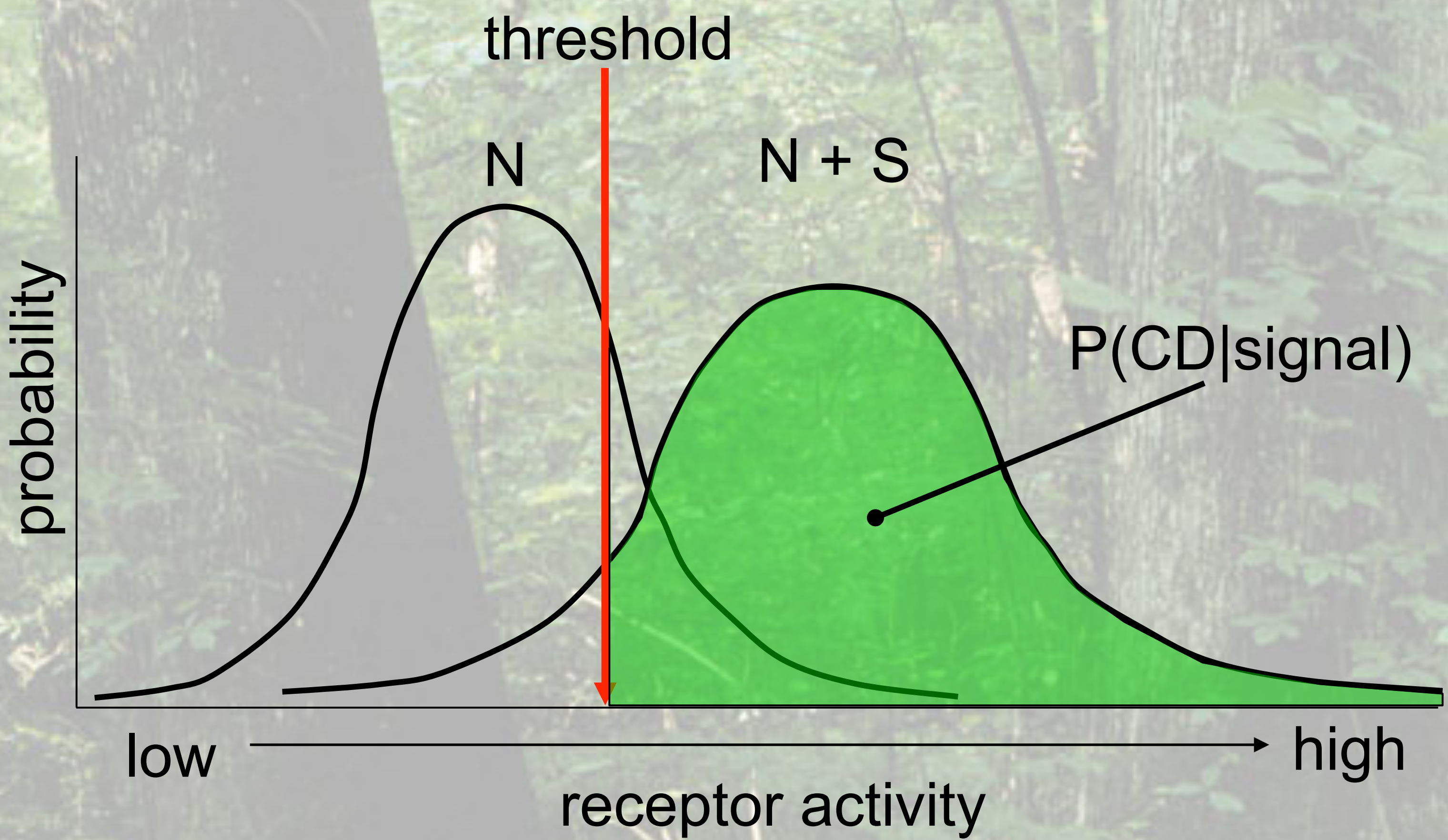
receiver's behavior has four possible outcomes . . .

- CD -- correct detection (signal, response)
- MD -- missed detection (signal but no response)
- FA -- false alarm (response but no signal)
- CR -- correct rejection (no signal, no response)

in the presence of noise, receiver's receptors do not completely separate noise+signal from noise alone



receiver's threshold sets the probabilities of the four possible outcomes



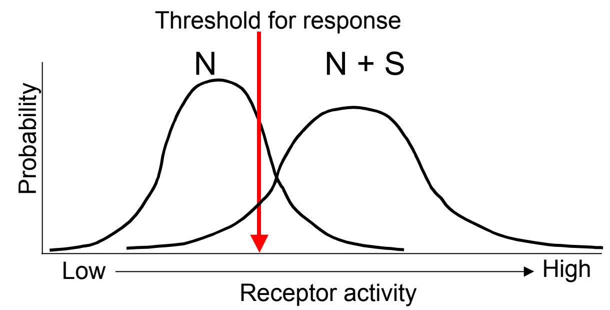
two of the possible outcomes are errors

		receiver's decision: response	receiver's decision: no response
signal	present	CORRECT DETECTION	MISSED DETECTION
signal	absent	FALSE ALARM	CORRECT REJECTION

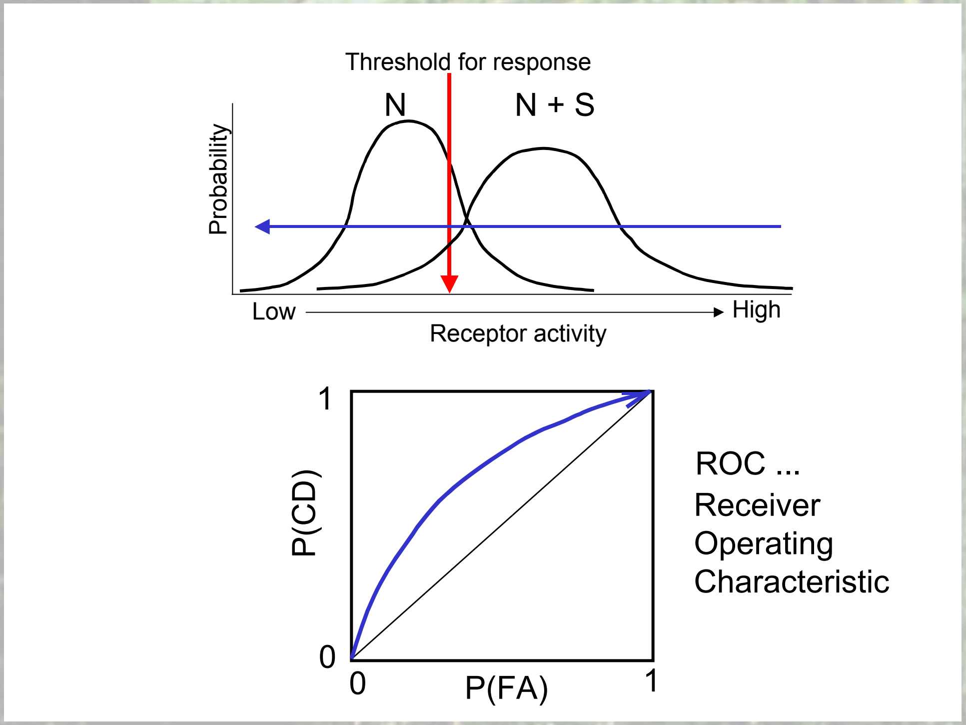
two kinds of errors are not independent

receivers cannot simultaneously minimize MD and FA

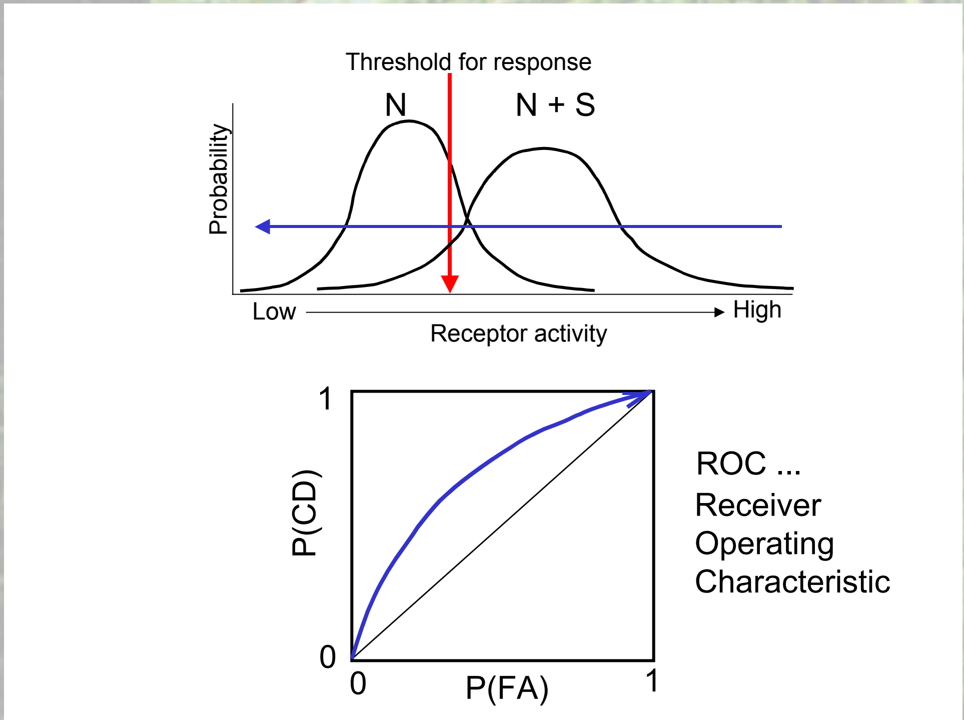
raising the threshold decreases FA, but increases MD
lowering the threshold has the opposite effects



receiver faces an inevitable trade-off



ROC -- p(CD) as a function of p(FA) -- describes this trade-off receiver faces an inevitable trade-off



receivers should evolve optimal thresholds utility (overall payoff) of any threshold for a receiver depends on . . .

(1) location of the threshold

(2) probability that a signal occurs when receiver samples its input

(3-6) payoffs for each of the four possible outcomes receiver's optimal threshold falls along a continuum between …

adaptive gullability . . .

low threshold for response . . .

decreases MD but allows more FA

adaptive fastidiousness . . .

high threshold for response . . .

decreases FA but allows more MD

Wiley 1994, 2000, 2006

E(U) = P(signal) * P(CD | signal) * U(CD) +
P(signal) * {1 - P(CD | signal)} * U(MD) +
{1 - P(signal)} * P(FA | no signal) * U(FA) +
{1 - P(signal)} * {1 - P(FA | signal)} * U(CR)

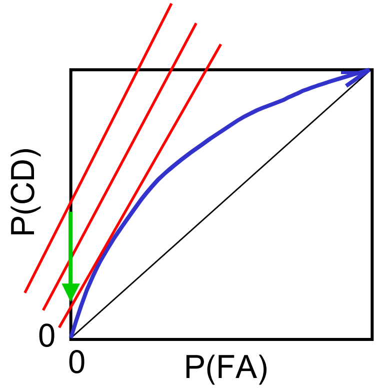
For any value of E(U) = U, we can rearrange this equation to obtain an indifference curve ...

$$P(CD) = \frac{(1 - s)(j - a)}{s(h - m)} P(FA) + s(j - m) - j + U$$

s = P(signal)

h, m, a, j = U(CD), U(MD), U(FA), U(CR)

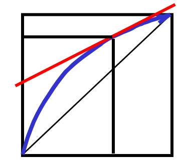
if we let U (which affects the y-intercept) vary, we can find the largest value of U possible for these conditions ...



Wiley 1994, 2000, 2006

alarm calls

$$\frac{(1 - s)(j - a)}{s(h - m)}$$



MD is costly

the slope is low when ...

s and h-m are high ... and j-a is low

for a receiver listening for true alarm calls
when some individuals occasionally give false alarm calls

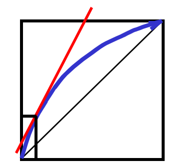
h >> 0 (avoiding predation)
m << 0 (exposure to predation)
j > 0 and a < 0 (a little time gained or lost feeding)

cryptic prey

or

optimal mates

$$\frac{(1 - s)(j - a)}{s(h - m)}$$



FA is costly

this value for the slope is high when ...

j-a is high ... and s and h-m are low

for a receiver searching for cryptic prey
or subtly discriminable objects such as optimal mates
when search costs are low ...

j and m > 0
(prospects for future success devalued by low cost of additional search)
h > j and m (optimal mate or appropriate prey)
a < 0 (suboptimal mate or inappropriate prey)

Wiley 1994, 2000, 2006

prevailing paradigm for evolution of communication

most previous treatments of receivers' errors . . .

just added variance to receivers' responses

prevailing paradigm for evolution of communication

most previous treatments of receivers' errors . . .

just added variance to receivers' responses

the result . . .

just substitute average payoffs for fixed payoffs

prevailing paradigm for evolution of communication

receiver is assumed to benefit from responding . . .

otherwise receiver would evolve not to respond

so signaling would not pay

and no communication would occur

receivers "must get what they want" . . . Grafen 1990b

prevailing paradigm for evolution of communication

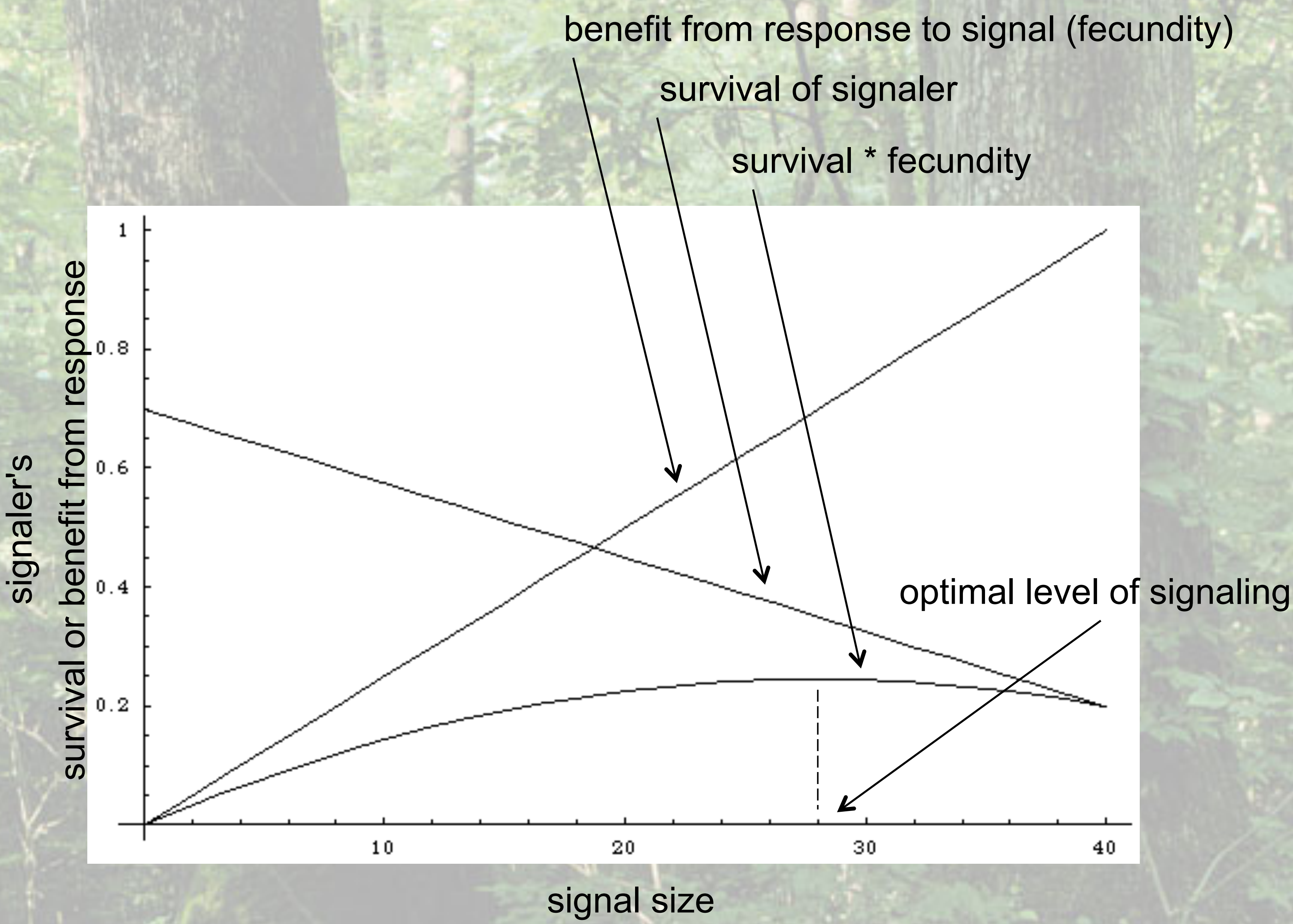
reliable (on average) signaling occurs

if and only if

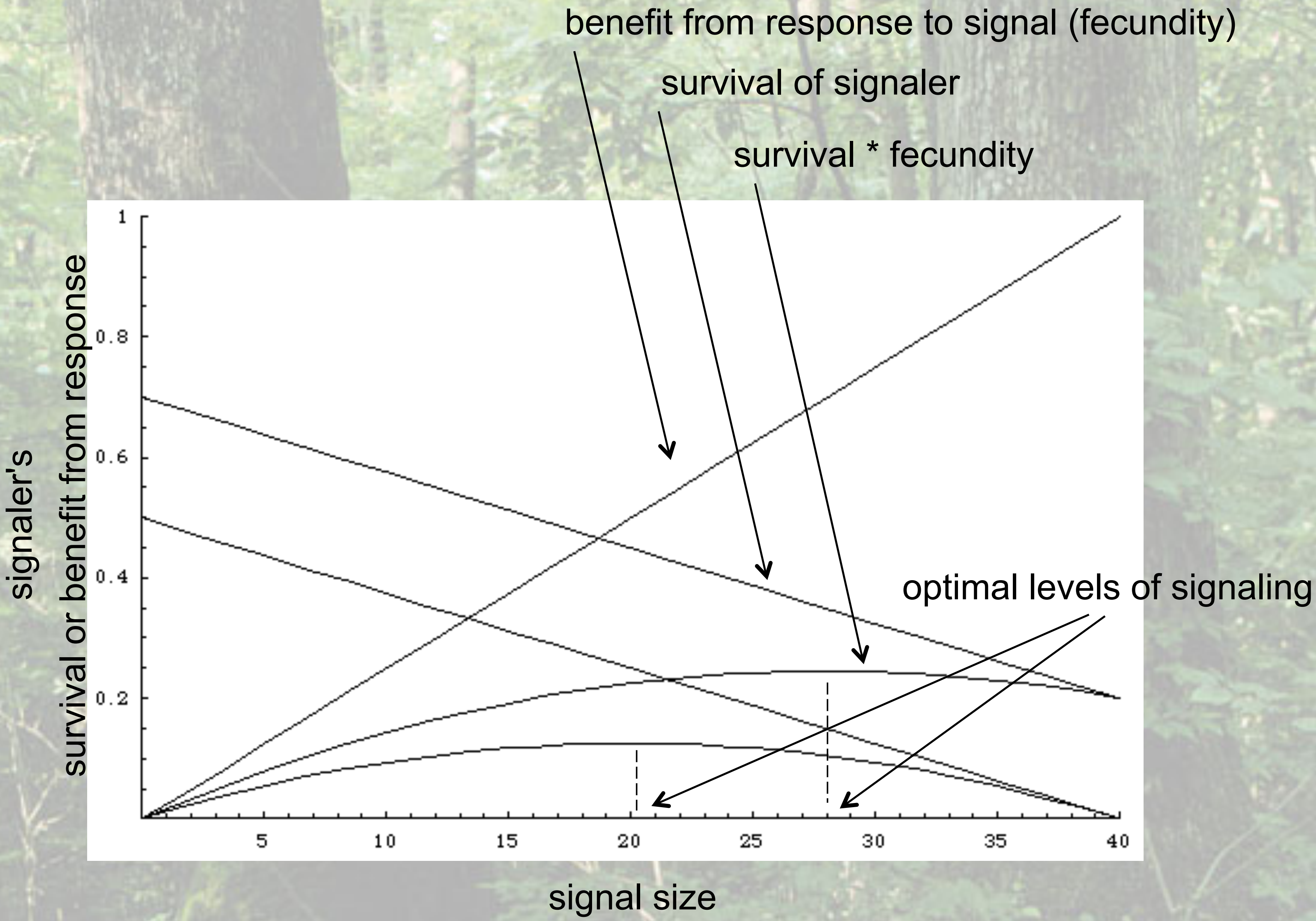
signals are costly and condition-dependent

Grafen (1990a,b) somewhat similar to Zahavi (1975)

prevailing paradigm for evolution of communication



prevailing paradigm for evolution of communication



prevailing paradigm for evolution of communication

receiver is largely out of the picture

after a few initial assumptions

signal-detection approach differs from the prevailing approach signal-detection paradigm

receivers' optimal performance depends on . . .

noise . . . but also the signal’s properties . . .

which depend on the signaler’s effort

signaler’s optimal effort depends on . . .

signal's cost . . . but also its benefit . . .

which depends on receiver's performance

signal-detection paradigm

receivers evolve in response to behavior of signalers

and

signalers evolve in response to behavior of receivers is there a joint optimum in communication . . .

a signal-detection equilibrium?

is there a joint optimum in communication . . .

a signal-detection equilibrium?

Signal-Detection Equilibrium (SDE) theory

instead of

Costly Condition-Dependent Signal (CCDS) theory

Signal-Detection Equilibrium: Basics

from receiver's perspective . . .

higher signal level favors higher optimal thresholds

because p(FA) decreases for any p(MD)

but as signal level increases . . .

higher thresholds have diminishing benefits

because p(CD) approaches 1.0

Signal-Detection Equilibrium: Basics

from signaler's perspective . . .

higher signal level requires . . .

greater exaggeration of signals . . .

and consequently greater effort

also results in greater receiver-dependent benefit

higher optimal thresholds of intended receivers result in . . .

higher probability of responses by receivers

these benefits have diminishing returns

because p(CD) approaches 1.0

marginal benefits . . . a decreasing function of effort

marginal costs . . . constant or increasing function of effort

Signal-Detection Equilibrium: Basics

if signalers adjust exaggeration of signals
(given current receivers' thresholds)

and receivers adjust thresholds
(given current exaggeration of signals)

result might be a signaler-receiver equilibrium

exaggeration of signals by signalers reaches an optimum

at which receiver performance also reaches an optimum

Signal-Detection Equilibrium: Doing the Math

signaler's optimal signal level =

snlevel | max(uS(sS(snlevel), th*(snlevel), bR, pS))

receiver's optimal threshold th* =

th | max(uR(payoff[outcomes], snlevel, th, pS))

snlevel, signal level in relation to noise

uS, signaler's utility

sS, signaler's survival

th, receiver's threshold (th*, optimal)

bR, signaler's benefit from a response

pS, probability of a signal

Signal-Detection Equilibrium: Doing the Math

signaler's optimal signal level =

snlevel | max(uS(sS(snlevel), th*(snlevel), bR, pS))

↓

receiver's optimal threshold th* =

th | max(uR(payoff[outcomes], snlevel, th, pS))

uR, signaler’s utility

Signal-Detection Equilibrium: Doing the Math

in Mathematica . . .

define the receiver's and signaler's utilities

find their maxima
across all possible signal levels

by finding the root of $\partial(\text{utility})/\partial(\text{signal level}) = 0$

Signal-Detection Equilibrium: Doing the Math

some assumptions and constants . . .

normal PDF's for noise alone (N) and signal+noise (SN)

mean | N = 0, sd | N = 1.0

mean | SN = signal level, sd | SN = sd | N = 1.0

uR = receiver's utility . . . defined earlier !

psR = p(receiver encounters a signal)

receiver's payoffs for mate-choice task . . .

dR = 2.0

mR = 0.9

fR = 0.1

rR = 1.0

Signal-Detection Equilibrium: Doing the Math

normal PDF's for noise alone (N) and signal+noise (SN)

mean | N = 0, sd | N = 1.0

mean | SN = signal level, sd | SN = sd | N = 1.0

uR = receiver's utility … defined earlier !

psR = p(receiver encounters a signal)

receiver's payoffs for mate-choice task . . .

dR = 2.0

mR = 0.9

fR = 0.1

rR = 1.0

Signal-Detection Equilibrium: Doing the Math

normal PDF's for noise alone (N) and signal+noise (SN)

mean | N = 0, sd | N = 1.0

mean | SN = signal level, sd | SN = sd | N = 1.0

uR = receiver's utility … defined earlier !

psR = p(receiver encounters a signal)

receiver's payoffs for mate-choice task . . .

dR = 2.0

mR = 0.9

fR = 0.1

rR = 1.0

Signal-Detection Equilibrium: Doing the Math

normal PDF's for noise alone (N) and signal+noise (SN)

mean | N = 0, sd | N = 1.0

mean | SN = signal level, sd | SN = sd | N = 1.0

uR = receiver's utility … defined earlier !

psR = p(receiver encounters a signal)

receiver's payoffs for mate-choice task . . .

dR = 2.0

mR = 0.9

fR = 0.1

rR = 1.0

Signal-Detection Equilibrium: Doing the Math

normal PDF's for noise alone (N) and signal+noise (SN)

mean | N = 0, sd | N = 1.0

mean | SN = signal level, sd | SN = sd | N = 1.0

uR = receiver's utility … defined earlier !

psR = p(receiver encounters a signal)

receiver's payoffs for mate-choice task . . .

dR = 2.0

mR = 0.9

fR = 0.1 ← false alarm is bad news!

rR = 1.0

see addendum (2) for an alarm-call task

Signal-Detection Equilibrium: Doing the Math

signaler's signal level $\propto$ signal exaggeration $\propto$

signaler's effort $\propto$ cost $\propto$ survival

Signal-Detection Equilibrium: Doing the Math

signaler's cost = sS / maxsS

survival relative to maximal survival (without signaling)

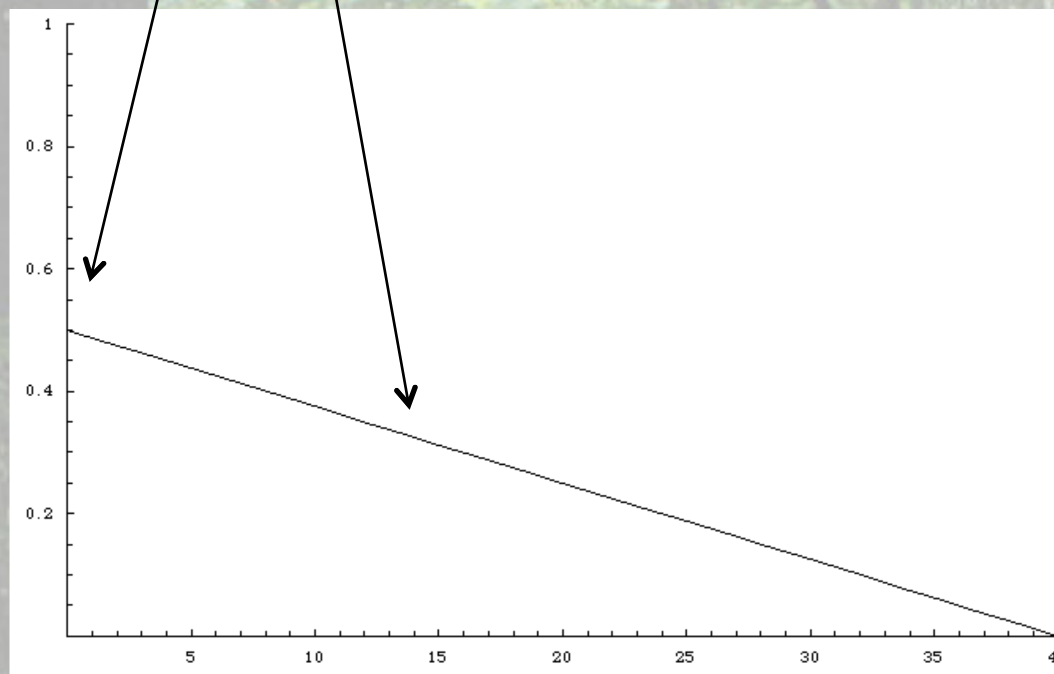
Signal-Detection Equilibrium: Doing the Math

signaler's cost = sS / maxsS

intercept = maximal survival of signaler (maxsS)

slope = marginal cost of exaggeration (mcX)

signaler's survival
sS



signal level

(signal exaggeration)

(signaling effort)

Signal-Detection Equilibrium: Doing the Math

signaler's benefit from receiver =

p[response by receiver] *

benefit (fecundity) for signaler from a response

any response outcome counts . . .

CD, correct detection of signal by receiver

FA, response when signaler present . . . despite absence of signal !

Signal-Detection Equilibrium: Doing the Math

signaler's utility =

survival * fecundity =

relativeSurvival = sS/maxsS

(p[signal] + p[no signal])

p[encounter] maxsS relativeSurvival benefit =

psS pe sS benefit + (1 - psS) pe maxsS benefit

when signal occurs maxsS cancels

when signal does not occur there is no cost (relativeSurvival = 1)

Signal-Detection Equilibrium: Doing the Math

to calculate signaler's utility for a particular signal level

first calculate *optimal threshold for receiver*

for this signal level

then calculate *utility for signaler*

for this signal level and this optimal threshold

Signal-Detection Equilibrium: Doing the Math

to calculate

optimal utility for the signaler

across all possible signal levels

use FindRoot(∂ uS / ∂ snlevel) Gracias, Mathematica!

for a set of conditions (constants) . . .

maxsS, mcX, bR	(payoffs for signaler)
pdR, pmR, pfR, pjR	(payoffs for receiver)
psS, peR	(signaling rate, encounter probability)

Signal-Detection Equilibrium: Doing the Math

signaler evolves

an optimal signaling effort (exaggeration, signal level)

conditioned on receiver evolving

an optimal threshold

in many cases, a signaler has an

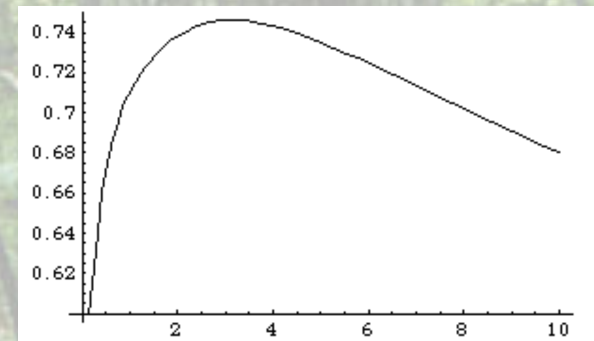
optimal level of signal exaggeration (effort, cost)

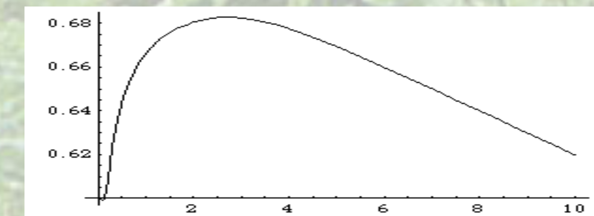
mate choice

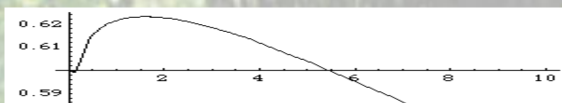
peR=0.5, maxsS=0.6, dR…=2.0,0.9,0,1.0

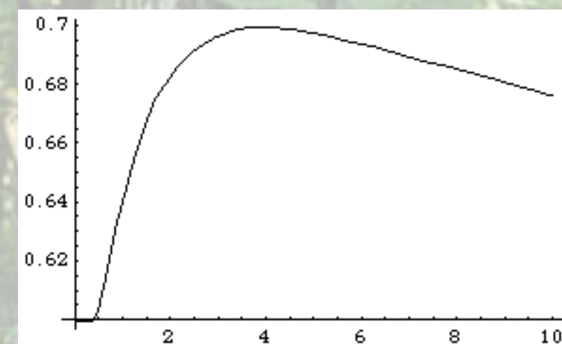
signaler's utility vs signal exaggeration

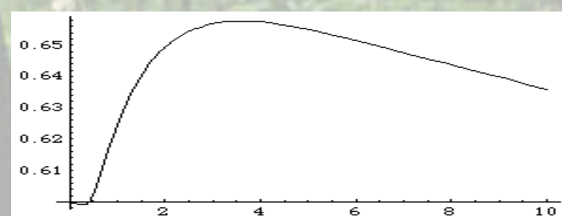
psS = 0.2, 0.5, 0.8

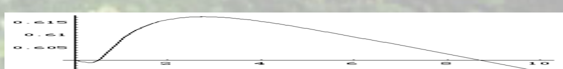


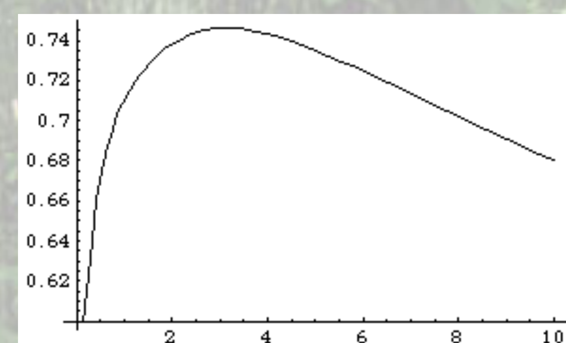


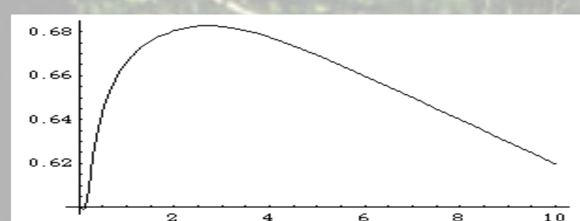


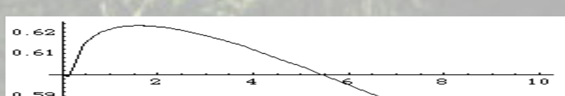








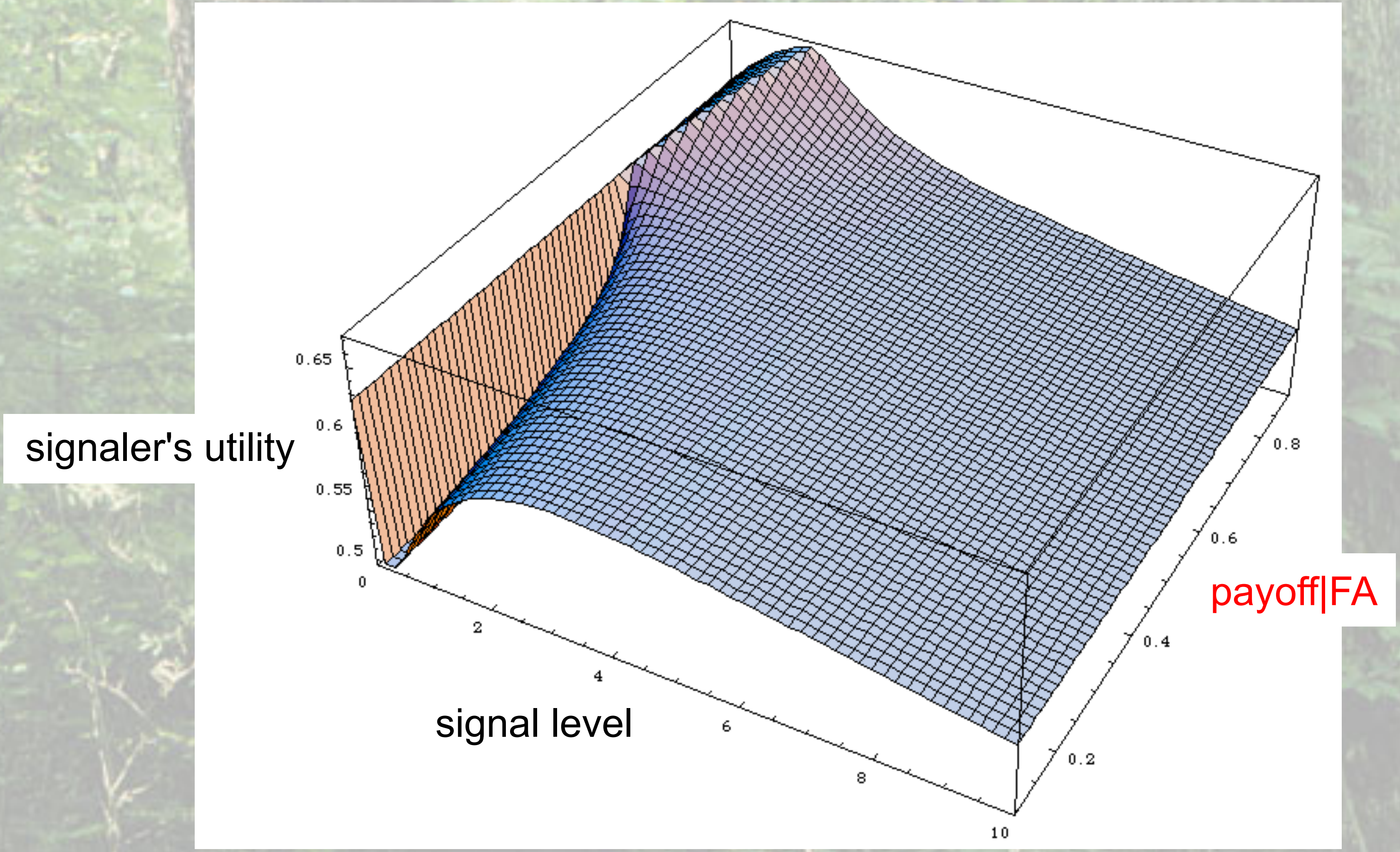




bR = 1.2, 1.5, 1.8

mate choice

signaler's utility vs signal level vs payoff|FA (fR)



Signal-Detection Equilibrium: Doing the Math

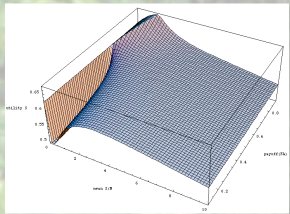
both receiver and signaler thus have

optima for performance

mate choice

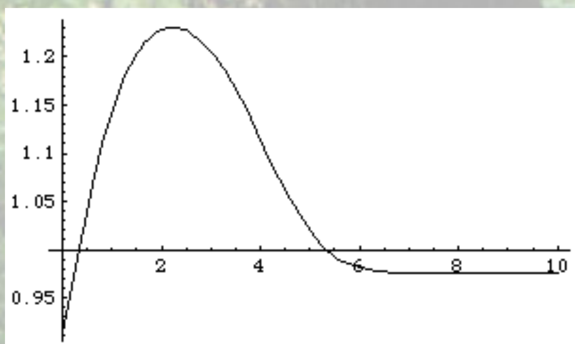
dR, mR, rR = 2.0, 0.9, 1.0

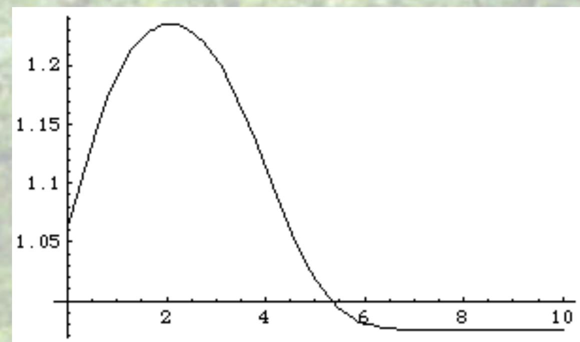
maxsS=0.5, bR=2.0, psS=0.5

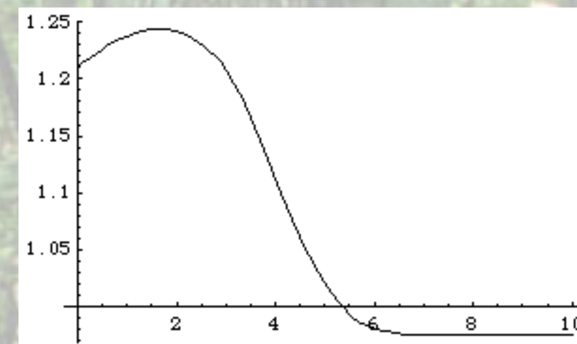


mate choice varies with cost of false alarm

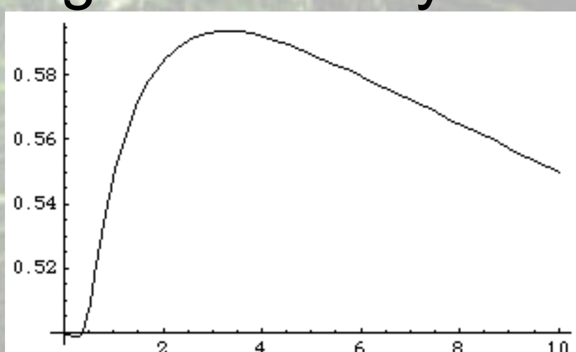
receiver's utility vs threshold

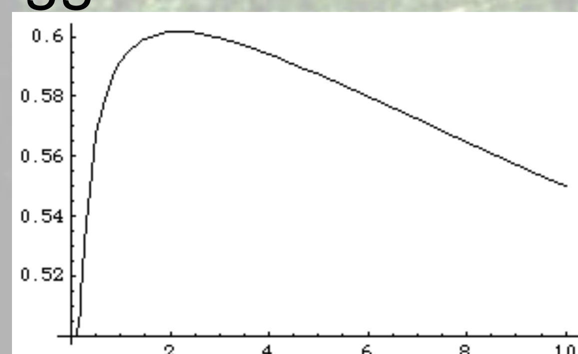


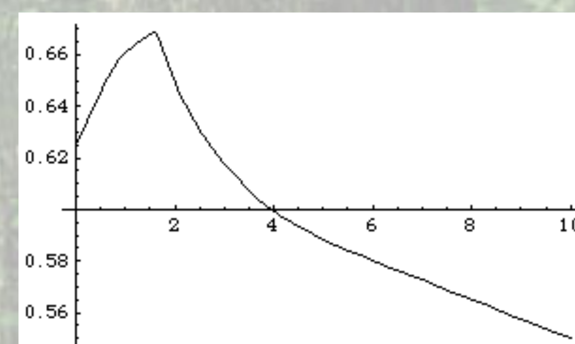




signaler's utility vs exaggeration







fR = 0.1, 0.5, 0.9

Signal-Detection Equilibrium: Conclusions

perhaps a general conclusion . . .

any adapting signaler-receiver system

in a particular situation

evolves toward

a joint optimum

for signaler efficiency and receiver performance

Signal-Detection Equilibrium: Conclusions

just as in costly condition-dependent signal CCDS theory,

signalers evolve an optimal effort

just as in signal-detection SD theory,

receivers evolve an optimal performance

Signal-Detection Equilibrium: Conclusions

signals do not reach maximal efficiency

(further exaggeration would improve probability of intended response)

responses to not reach maximal performance

(further exaggeration would reduce errors)

Signal-Detection Equilibrium: Conclusions

evolution does not result in perfect communication

signalers will not

always produce signals with the intended effect

receivers will not

always avoid errors

Signal-Detection Equilibrium: Conclusions

signalers are always subject to . . .

unresponsive and unintended receivers

receivers with different constraints on performance

(eavesdroppers, rivals)

can always evolve responses to exploit signalers

Signal-Detection Equilibrium: Conclusions

receivers are always subject to deception

they do not always "get what they want"

signalers with different constraints on signaling
can always evolve signals to exploit receivers

deception is an exception to the rule of "continuity in everything"

Signal-Detection Equilibrium: Conclusions

Krebs and Dawkins (1985) were correct ...

manipulation is an unavoidable consequence of communication

but reliability is the predominant feature of communication

Signal Detection Equilibrium theory

avoids some weaknesses of CCDS theory

(1) qualitative predictions that reliable signaling has costs for signalers and benefits for receivers are not strong predictions

- all signals have some costs
  - cost-free signals are difficult to imagine
- all responses have benefits on average
  - otherwise responses cannot evolve by selection

alternative hypotheses . . .

are indistinguishable from the null hypothesis . . .

communication is non-adaptive . . .

evolves by random processes . . . rather than by selection

(2) CCDS theory predicts misleading costs for signalers

because CCDS theory does not take into account
adaptive adjustments by receivers

Signal Detection Equilibrium theory

predicts optimal costs for signalers
that take into account adaptive adjustments by receivers

Signal Detection Equilibrium theory

focus on signals in noise results in predictions about the amount and the direction of signal exaggeration

exaggeration of signals should

- increase performance of intended receivers
- decrease performance of *un*intended receivers

because noise varies across environments

- signals should adapt to the environment

Signal Detection Equilibrium theory

signals should evolve to *minimize* costs

for any increase in performance of intended receivers

signalers should evolve to *maximize* efficiency of signaling

increased costs are only incidental

Signal Detection Equilibrium theory

focus should be on efficiency of signals

$$\text{efficiency of signaling} = \frac{(\text{ benefits from signaling} * \text{survival of signaler })}{(\text{ benefits without signaling} * \text{survival without signaling })}$$

focus solely on the costs of signals is misdirected

Signal Detection Equilibrium theory

predicts possibilities for manipulation

by unresponsive and unintended receivers

(subject to different constraints on performance
in comparison to intended receivers)

by deceptive signalers

(subject to different constraints on signaling
in comparison to preferred signalers)

Signal Detection Equilibrium theory

evolution of communication is more complicated than "costs of signals" and "benefits to receivers"

Signal Detection Equilibrium theory

neglected variables include . . .

probabilities and payoffs of all four outcomes for receivers

probabilities of signals (when receiver is attending)

probabilities of responses

by intended receivers
by unintended receivers

payoffs for signaling as a function of effort

from each category of receiver

all of these measures … in different environments

Signal Detection Equilibrium theory

neglected variables include . . .

probabilities and payoffs of all four outcomes for receivers

probabilities of signals (when receiver is attending)

probabilities of responses

by intended receivers
by unintended receivers

payoffs for signaling as a function of effort

from each category of receiver

all of these measures … in different environments

Signal Detection Equilibrium theory

neglected variables include . . .

probabilities and payoffs of all four outcomes for receivers

probabilities of signals (when receiver is attending)

probabilities of responses

by intended receivers
by unintended receivers

payoffs for signaling as a function of effort

from each category of receiver

all of these measures … in different environments

Signal Detection Equilibrium theory

neglected variables include . . .

probabilities and payoffs of all four outcomes for receivers

probabilities of signals (when receiver is attending)

probabilities of responses

by intended receivers
by unintended receivers

payoffs for signaling as a function of effort

from each category of receiver

all of these measures … in different environments

Signal Detection Equilibrium theory

neglected variables include . . .

probabilities and payoffs of all four outcomes for receivers

probabilities of signals (when receiver is attending)

probabilities of responses

by intended receivers
by unintended receivers

payoffs for signaling as a function of effort

from each category of receiver

all of these measures … in different environments

mathematical exploration of the joint optima of receivers' performance and signalers' effort *has just begun!*

stay tuned !

http://www.unc.edu/~rhwiley

Signal Detection Equilibrium theory

addendum (1)

what is a signal?

the essential feature of signals
determines the essential features of communication

Signal Detection Equilibrium theory

a signal is a pattern of energy (or matter)

that elicits a response from a receiver

but does not provide all of the power for the response

Signal Detection Equilibrium theory

because a signal does not provide all of the power for a response . . .

a receiver is a mechanism that . . .

associates signals with responses

it requires . . . transducers, gates, amplifiers, effectors

for instance . . . receptors, cns, musculo-skeletal system

Signal Detection Equilibrium theory

because a signal does not provide all of the power for a response . . .

receiver is in control -- at least of the response

but receiver is also exposed

because receiver uses low-power signals for decisions

receiver is inevitably subject to constraints
on detecting and discriminating signals in noise

. . . open to possibilities of signals from unexpected signalers

. . . inherently open to the possibility of deception

Signal Detection Equilibrium theory

signaler is also in control -- at least of the signal

but signaler is also exposed

because the signaler relies on receivers' power and decisions

signaler is inevitably subject to constraints

on directing signals to intended receivers

. . . open to possibilities of unresponsive/unintended receivers

. . . inherently open to the possibility of eavesdropping

Signal Detection Equilibrium theory

no need for a distinction between signal and index

insufficient power of a signal is enough

no need for a specialized communicative function for a signal

predictable responses by a receiver are enough

definition of a signal applies to all communication (all signaling)

electronic, organismal, cellular, molecular

nevertheless . . .

Signal Detection Equilibrium theory

evolving (living) signalers and receivers
have a special property . . .

both signaling and receiving should evolve
to maximize the utility of each

caveat -- we should not expect
all organisms to have reached an adaptive optimum

maladaptive (nonadaptive) behavior can result from

- conditions changing faster than adaptation
- genetic drift
- migration from populations in other environments
- genetic or developmental constraints
  (valleys in the adaptive landscape)

because SDE theory makes quantitative predications about the
direction and level of exaggeration of signals
and the performance of receivers . . .
the adaptedness of communication becomes an empirical question

Signal Detection Equilibrium theory

the biological/psychological questions are ...

how should signaling and receiving evolve
so signalers and receivers reach optimal performance?

because evolution of optimal performance is evolutionary adaptation …

what features should adapted communication have
in different environmental conditions?

Signal Detection Equilibrium theory

addendum (2)

optima for receiver's performance and signaler's effort
for alarm calls

receiver's payoffs for alarm calls . . .

dR = 2.0

mR = 0.1 ← missed detection is bad news!

fR = 0.9

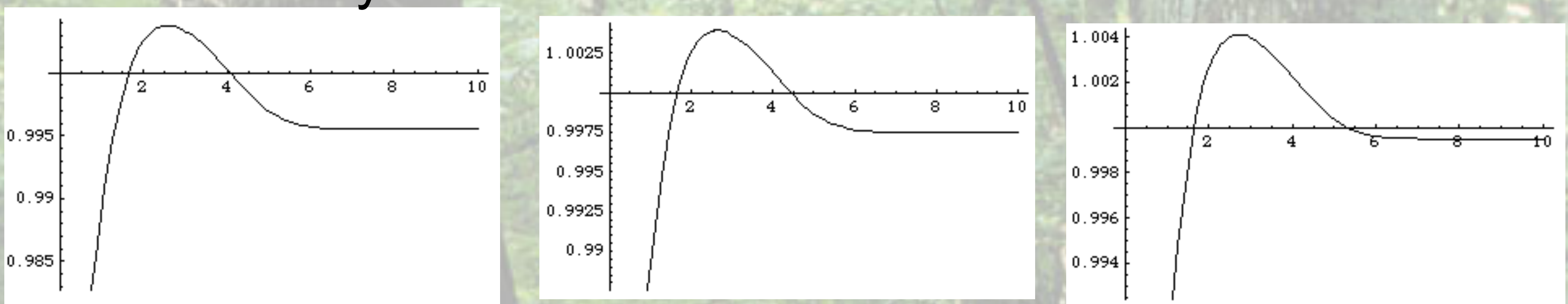
rR = 1.0

dR, fR, rR = 2.0, 0.1, 1.0

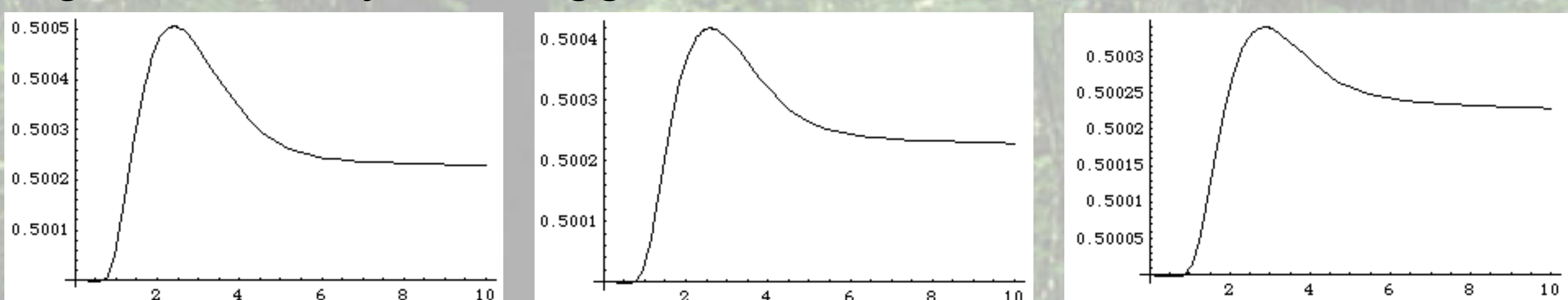
maxsS=0.5, bR=1.1, psS=0.01

alarm call varies with cost of missed detection

receiver's utility vs threshold

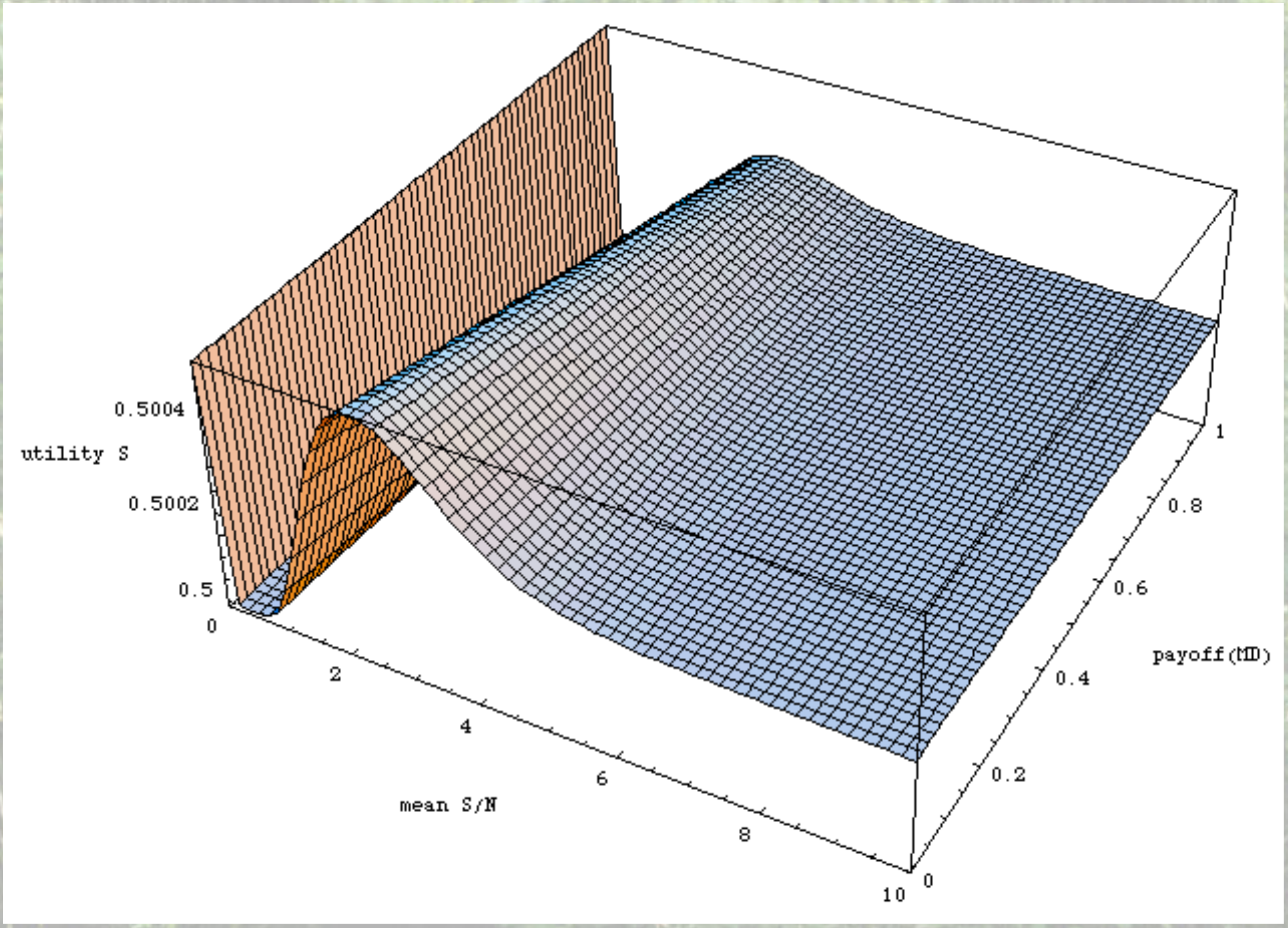


signaler's utility vs exaggeration



mR = 0.1, 0,5, 0.9

signaler's utility vs exaggeration vs mR (payoff|MD)



Big Oak Woods, N.C. Botanical Garden, University of North Carolina, Chapel Hill