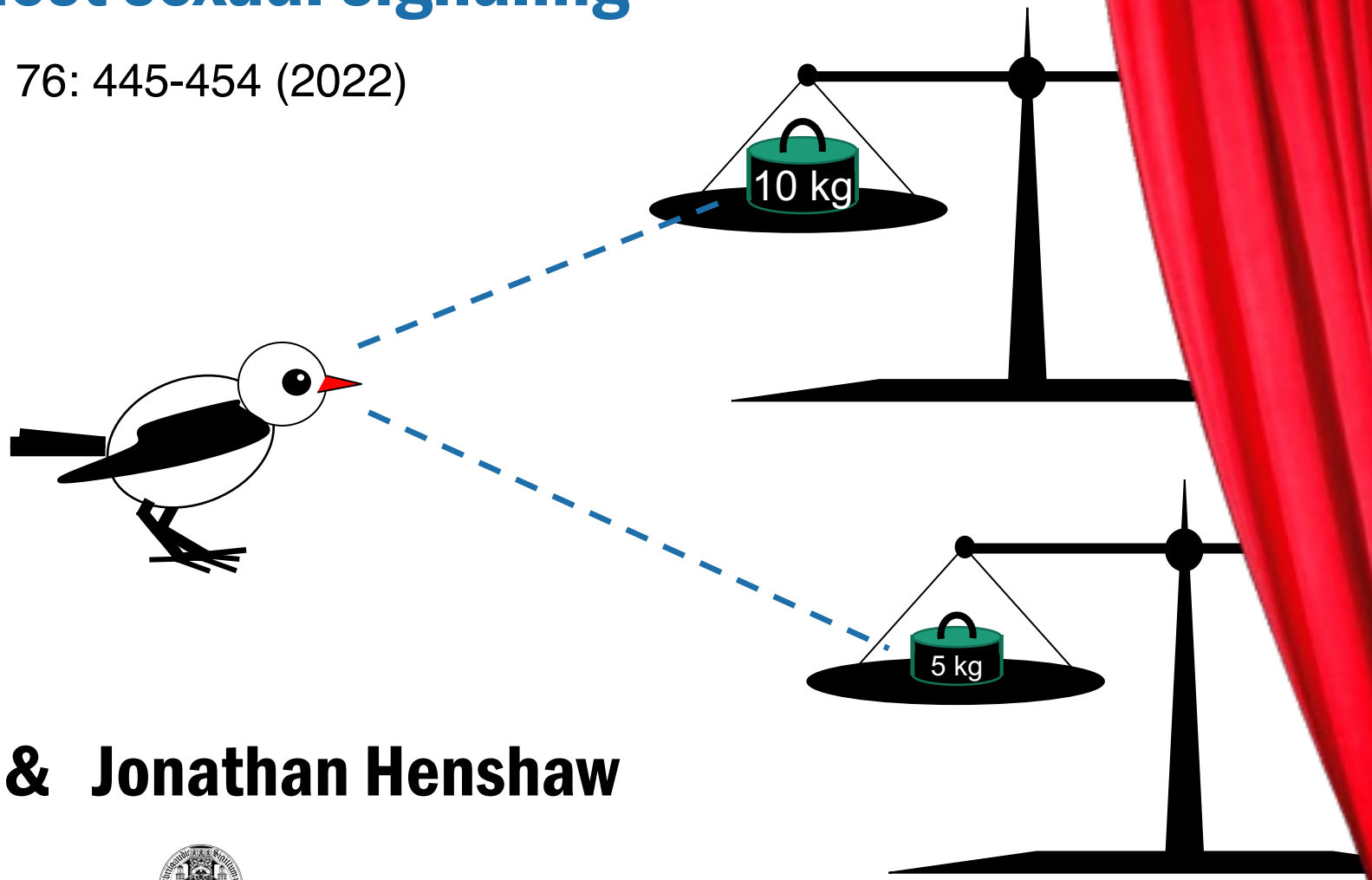
The balance model

of honest sexual signaling

Evolution 76: 445-454 (2022)



Lutz Fromhage & Jonathan Henshaw

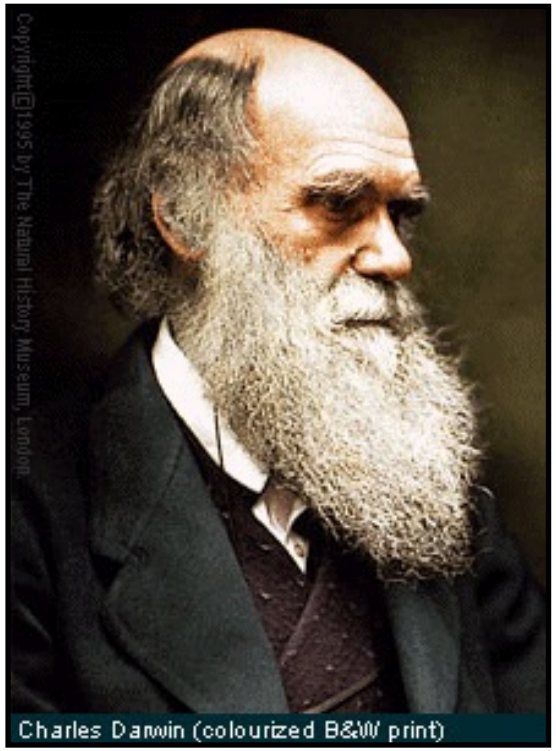
JYVÄSKYLÄN YLIOPISTO
UNIVERSITY OF JYVÄSKYLÄ

ALBERT-LUDWIGS-
UNIVERSITÄT FREIBURG

sex differences: coloration, ornamentation

blue bird of paradise

anolis lizard



Darwin 1871

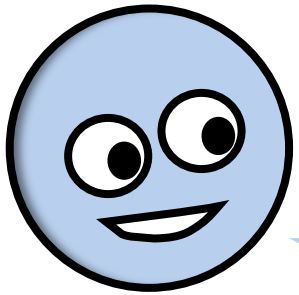
Sexual selection, including female choice.

benefits of female choice

heritable
genetic (‘indirect‘)

non-heritable
non-genetic ('direct‘)

e.g. “good genes” for viability
and/or attractiveness



Why should signals of quality be 'honest'?

Handicap hypothesis

- male ornament = handicap

  costly to produce and/or detrimental to survival

- only high quality males can afford the cost of exhibiting the handicap

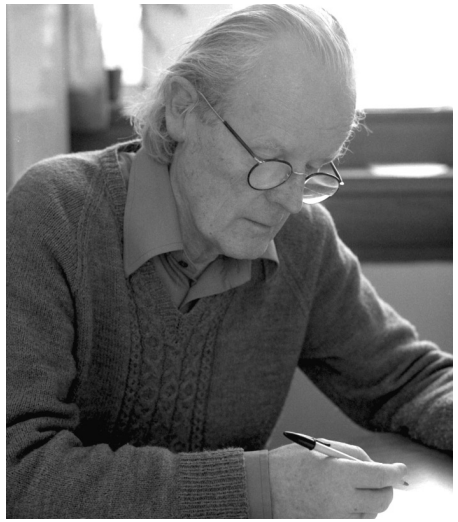
  → cheat-proof signal of quality

Zahavi 1975

Controversy

doesn't work if offspring inherit both handicap + ‘good genes’

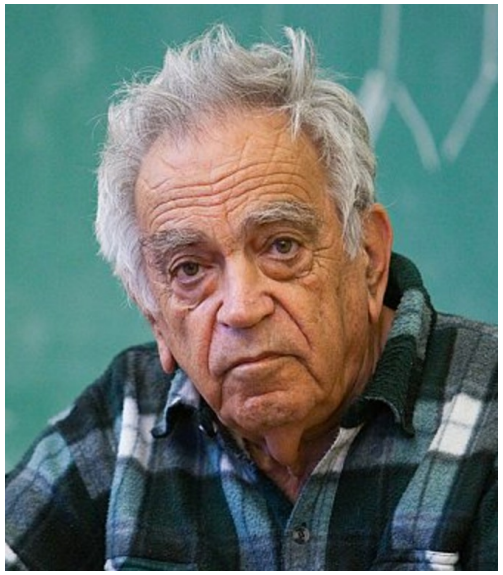
Maynard Smith (& others) in 70’s/80’s



works if trait expression is *condition-dependent*

Grafen 1990

Controversy



Zahavi 1981, 1987, 1997:

‘Handicap’ selection = selection for *waste*, not efficiency.
Ornaments evolve *because* they are costly, not *in spite of* it.

Getty 2006:

- Ornament = *investment* in mating success (≠ waste)
- Mutations that reduce the cost will spread

BIOLOGICAL REVIEWS

Cambridge Philosophical Society

Biol. Rev. (2020), **95**, pp. 267–290.
doi: 10.1111/brv.12563

The Handicap Principle: how an erroneous hypothesis became a scientific principle

Dustin J. Penn[1]* and Szabolcs Számadó[2,3,4]

"There is no theoretical or empirical support for the Handicap Principle and the time is long overdue to usher this idea into an 'honorable retirement' ".

[…reboot…]

invested resources

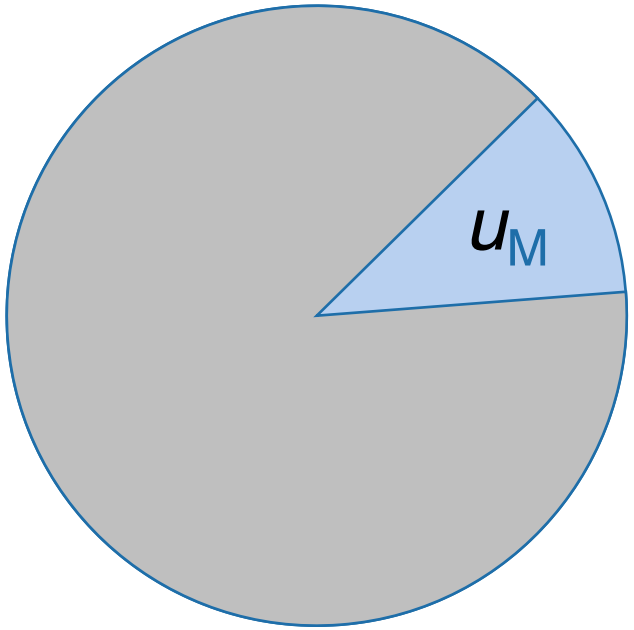
Fitness = $M(u_M)$ * $L(u_L)$

mating rate lifespan

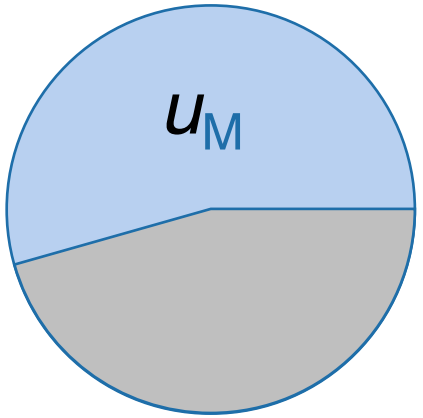
Total resources:

$$R = u_M + u_L$$

resources R = "individual quality"

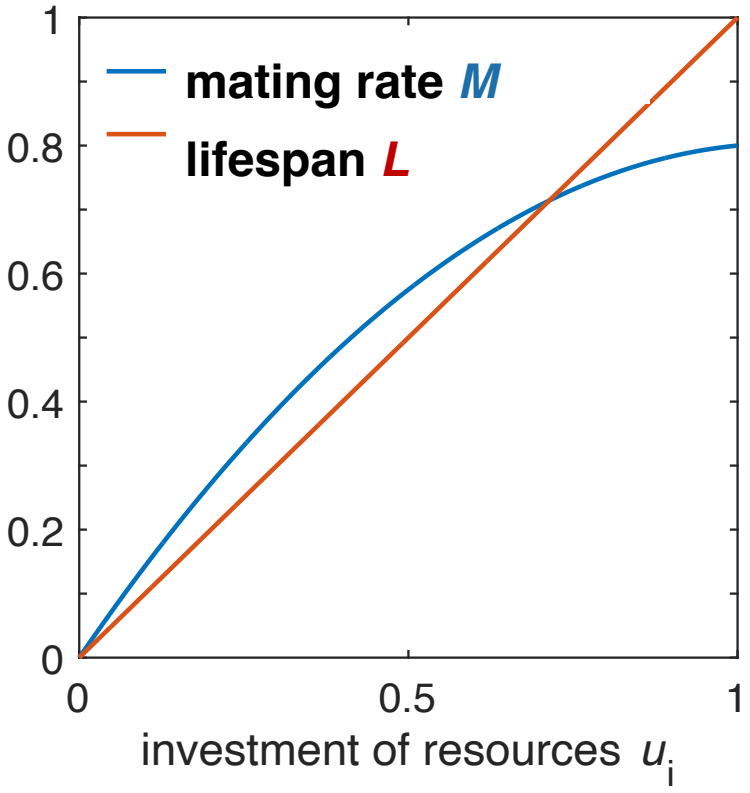


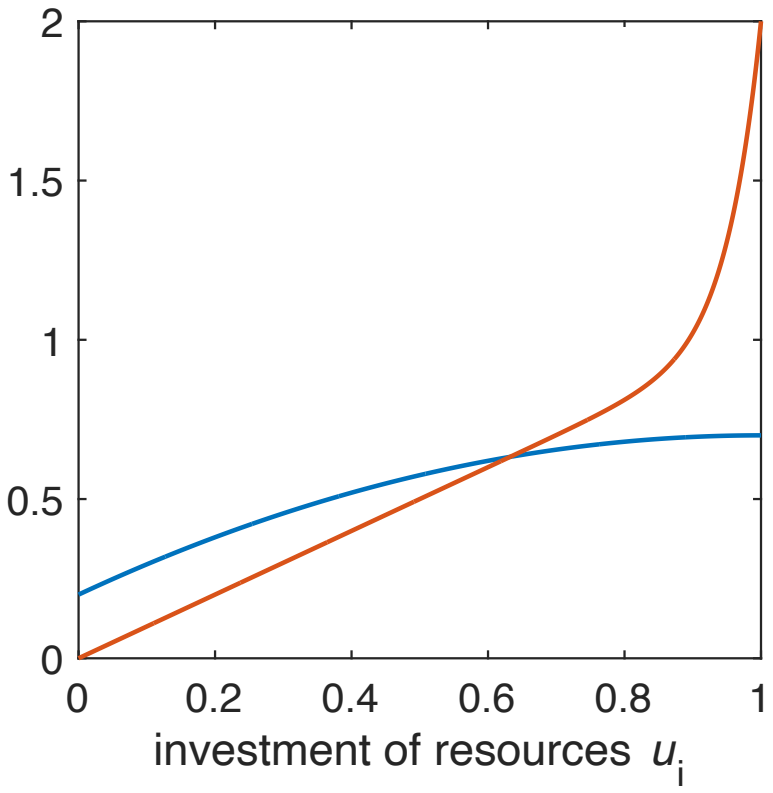
high quality male investing
little in mating success



low quality male investing
much in mating success

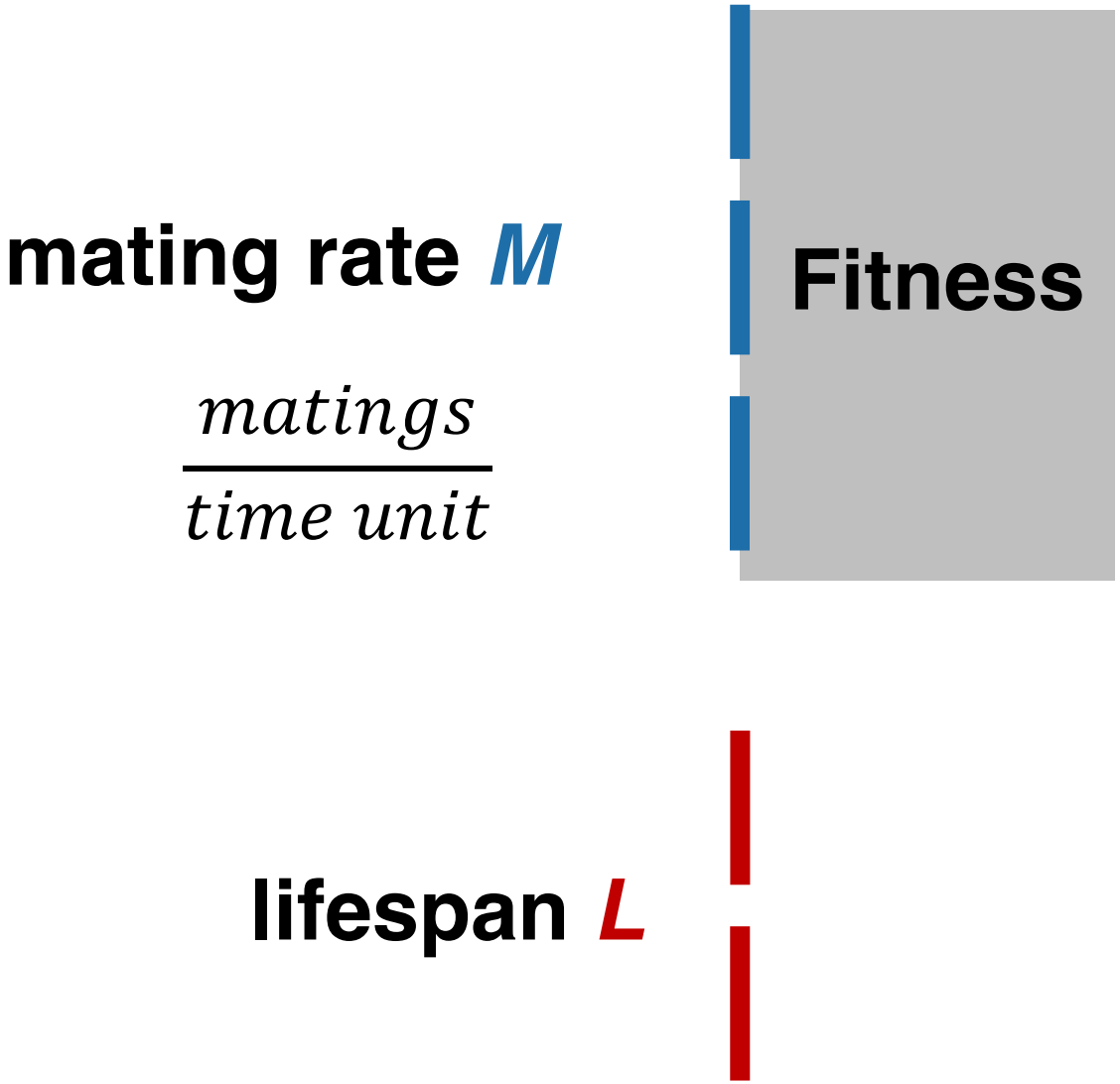
$M(u_M)$, $L(u_L)$ functions: examples





mating rate *M*

$$\frac{matings}{time\ unit}$$

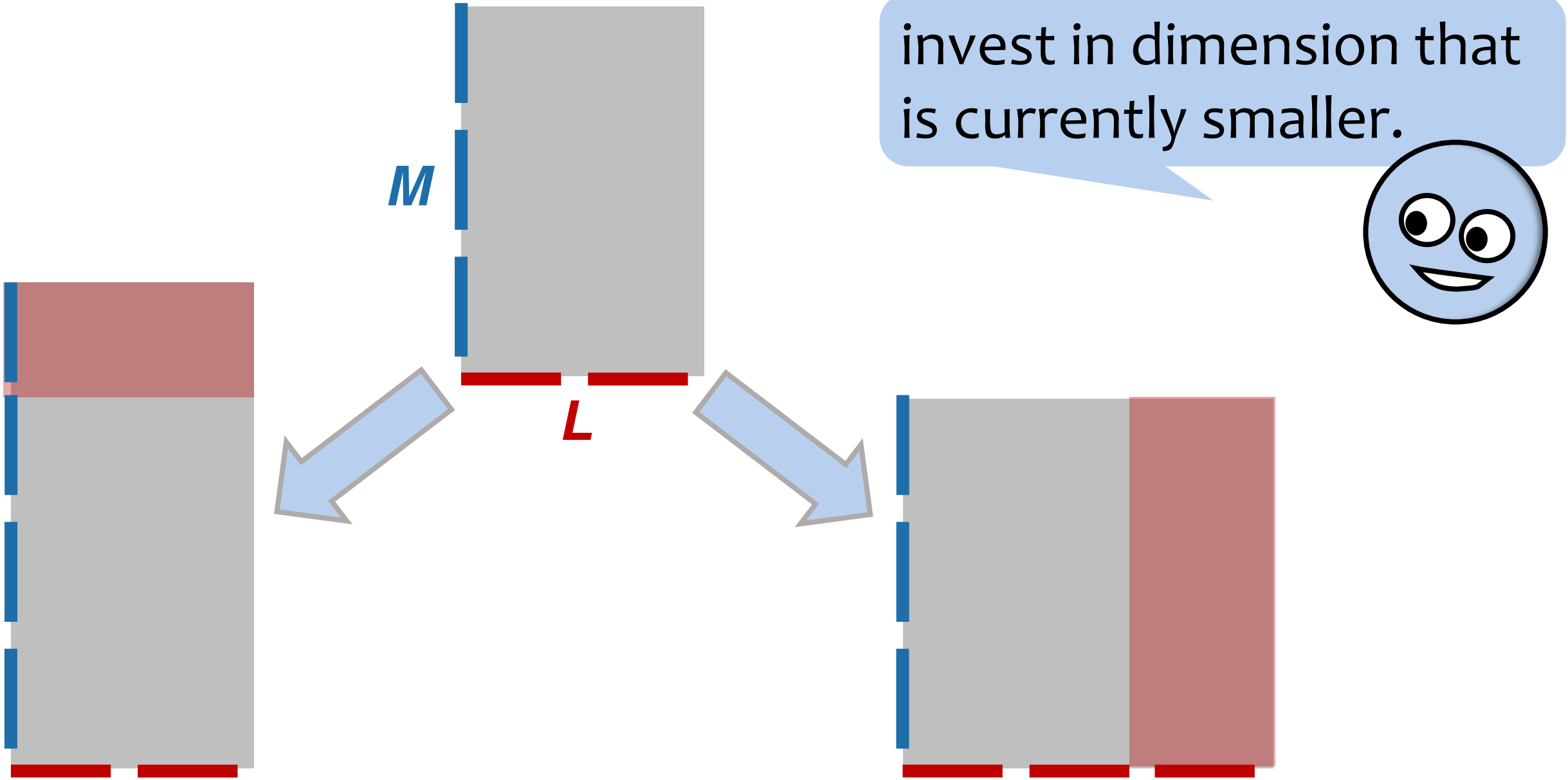

mating rate M
$\frac{matings}{time\ unit}$
Fitness
lifespan L

mating rate *M*

lifespan *L*

What should you do?

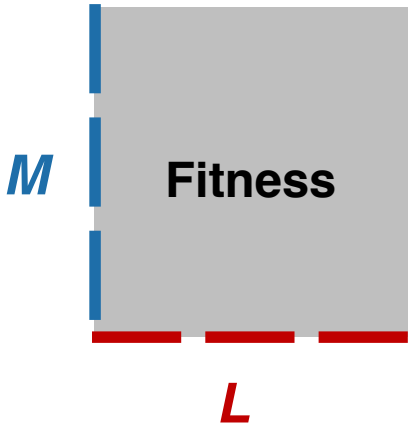
Suppose you can invest + 1 unit (either —— or ——)
into either dimension.

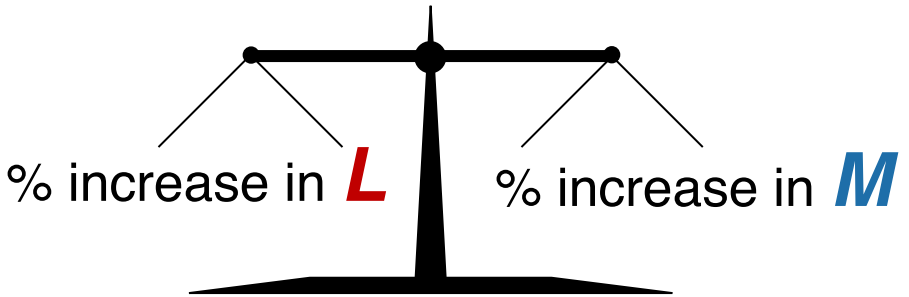


Option 1: invest in *M*

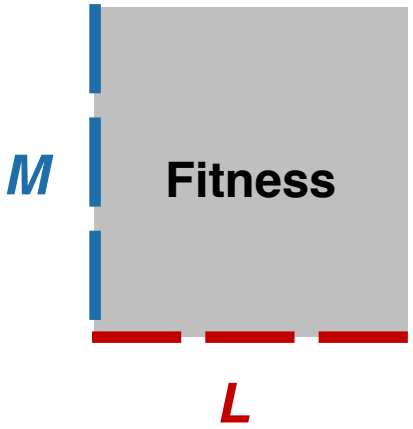
Option 2: invest in *L*

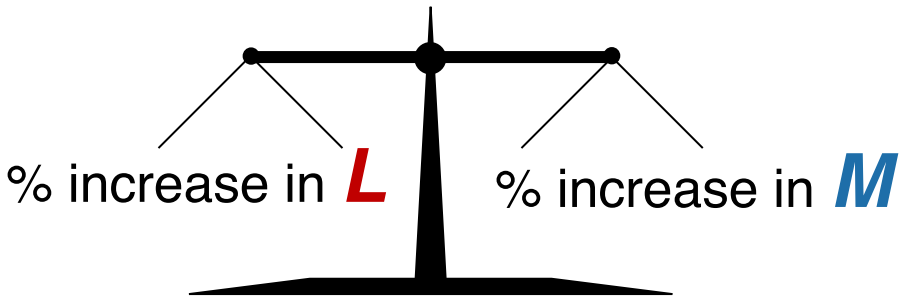
Optimal allocation:





Optimal allocation:





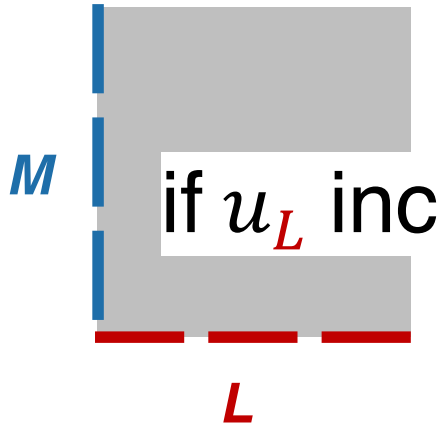
$$\frac{L'(u_L)}{L(u_L)} = \frac{M'(u_M)}{M(u_M)}$$

s_L s_M

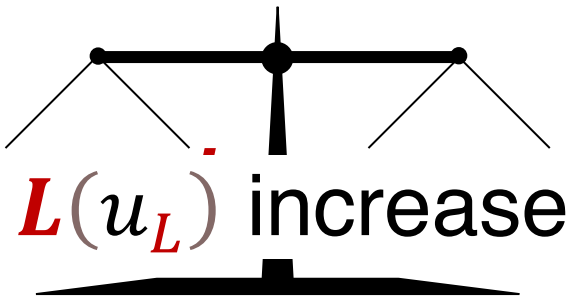
selection gradients:

(for investing in *L* and *M*)

Optimal allocation:



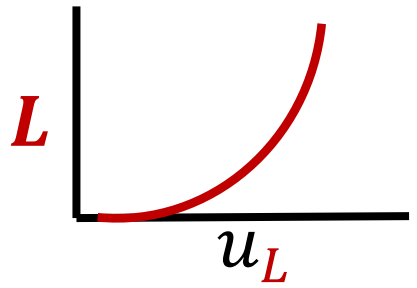
if u_L increases → $L(u_L)$ increases → S_L decreases



$$\frac{L'(u_L)}{L(u_L)} = \frac{M'(u_M)}{M(u_M)}$$

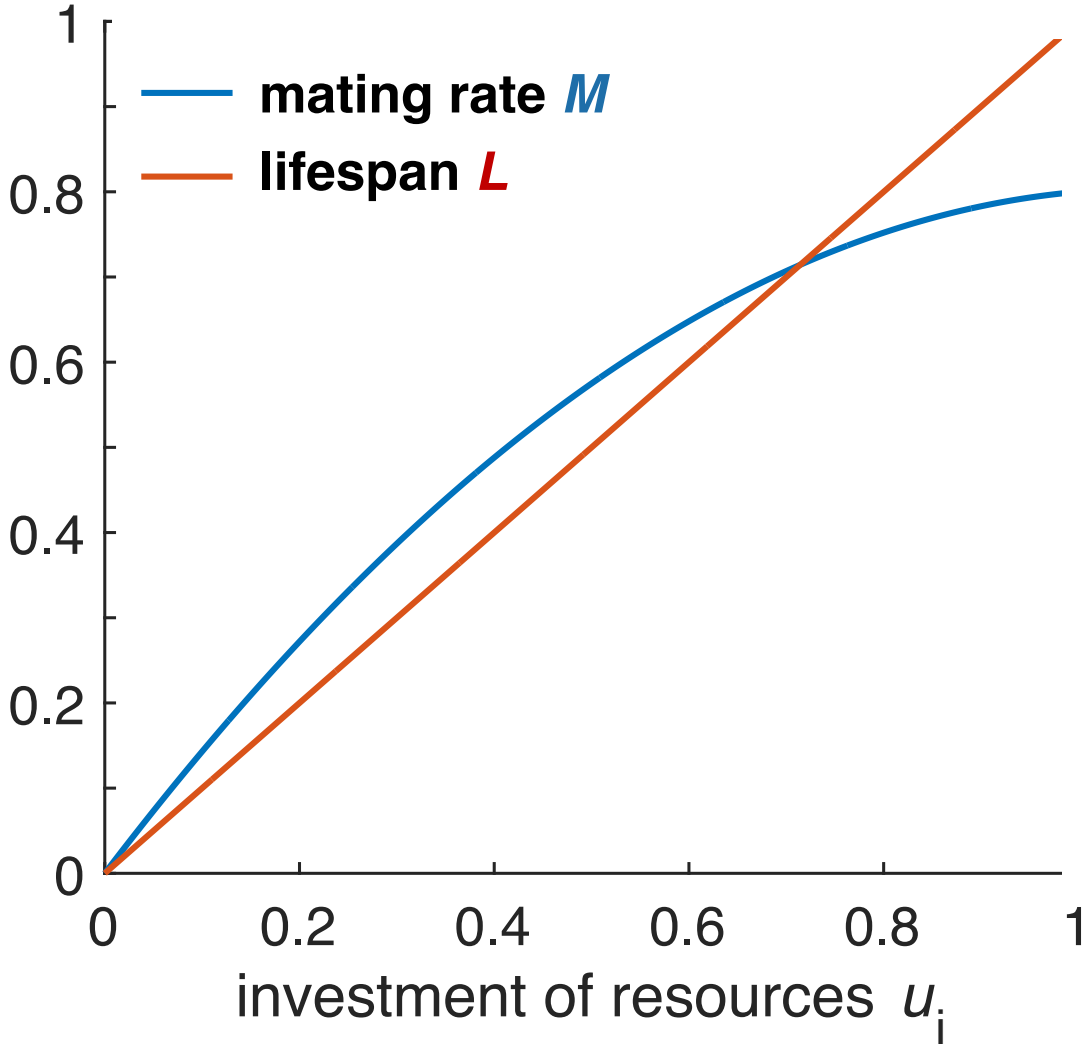
S_L

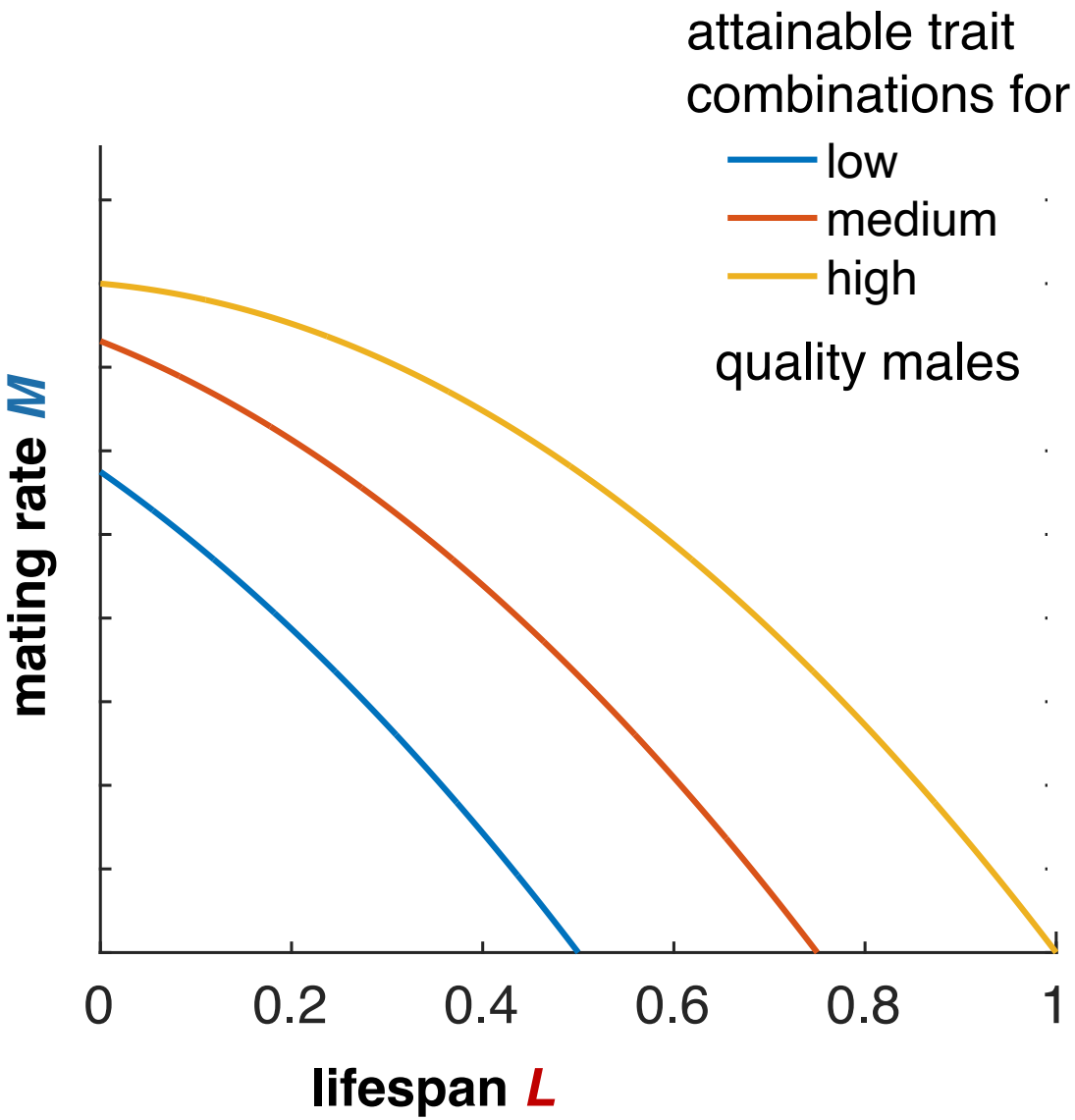
(unless compensated by increasing $L'(u_L)$)

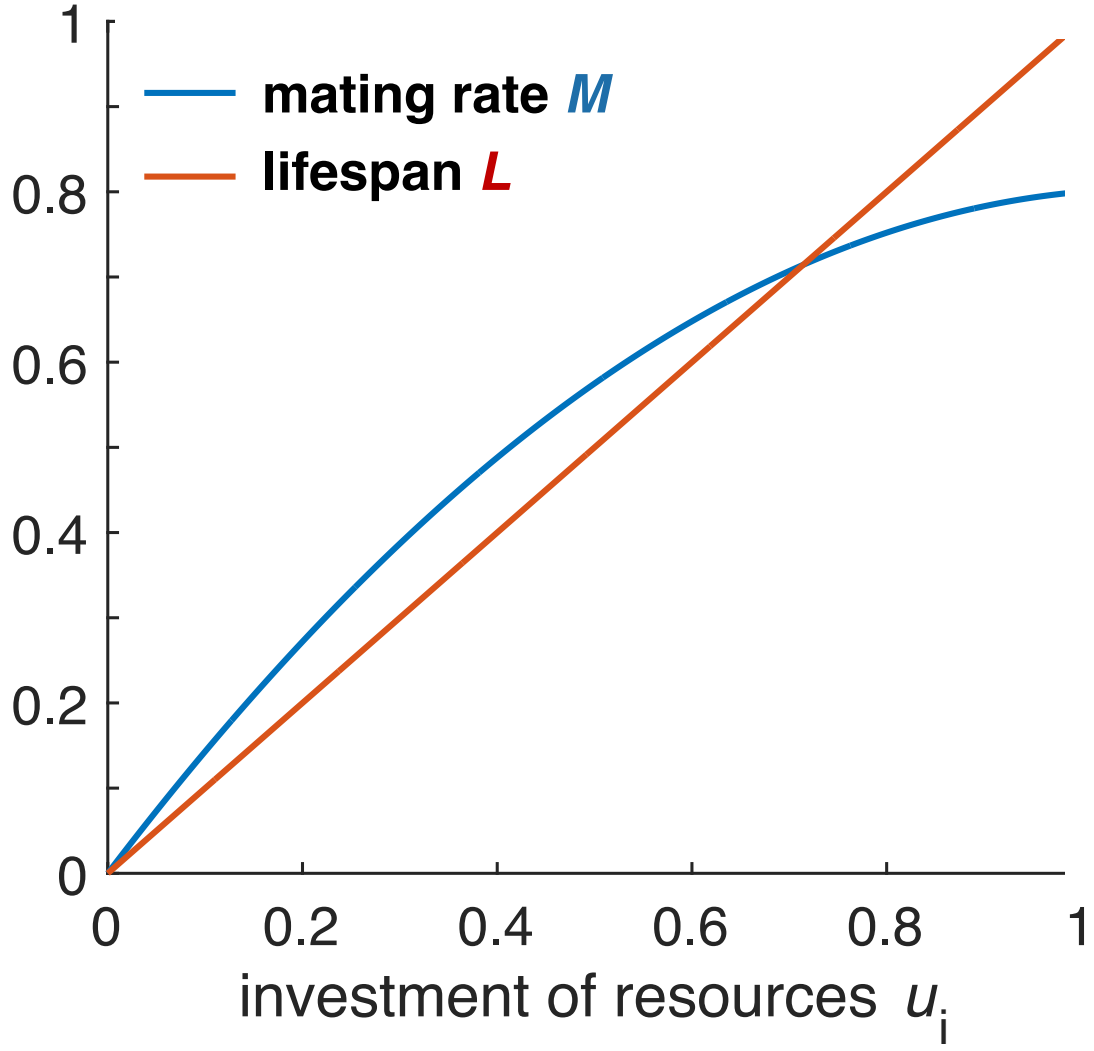


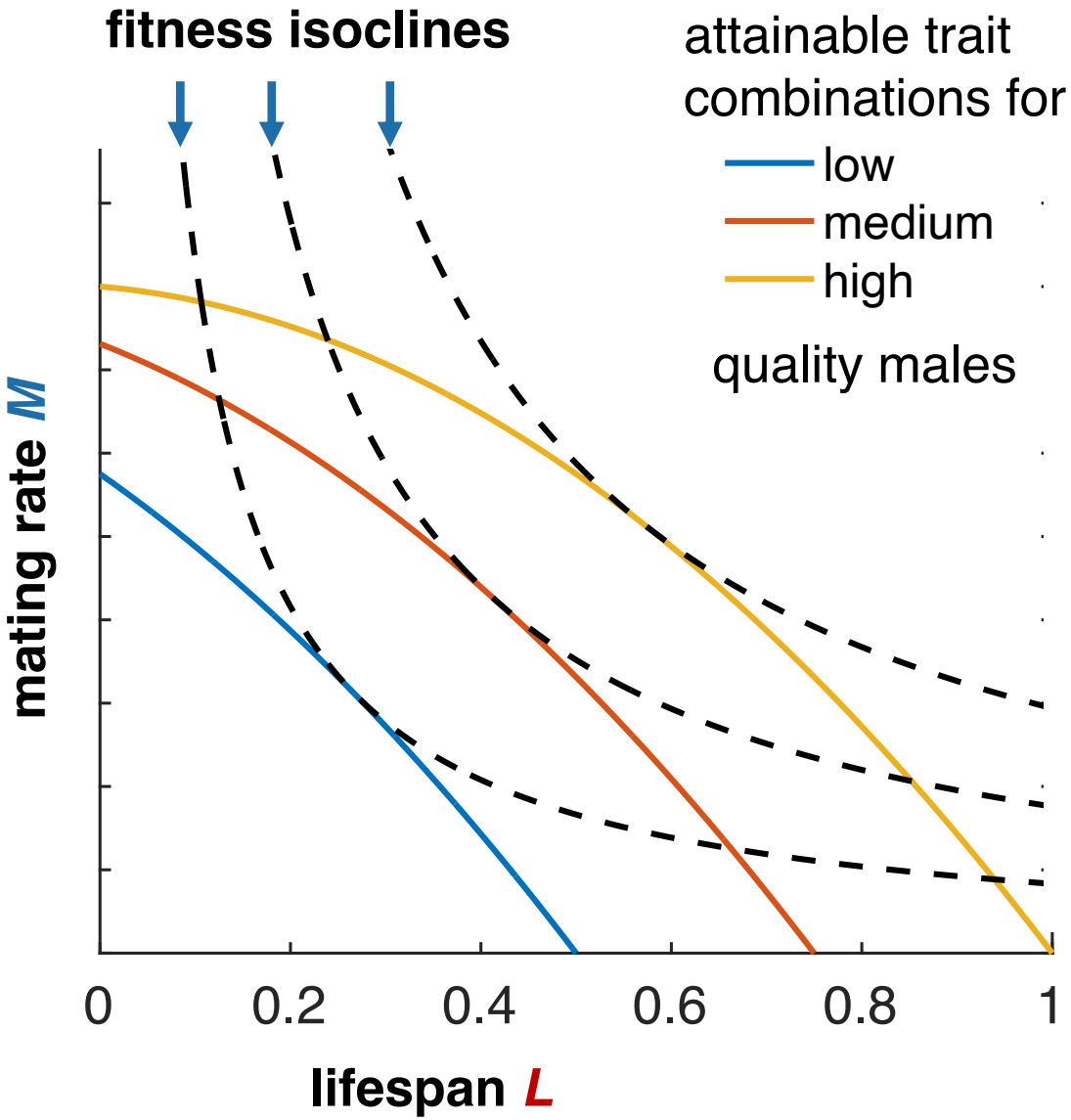
Honest signalling theorem

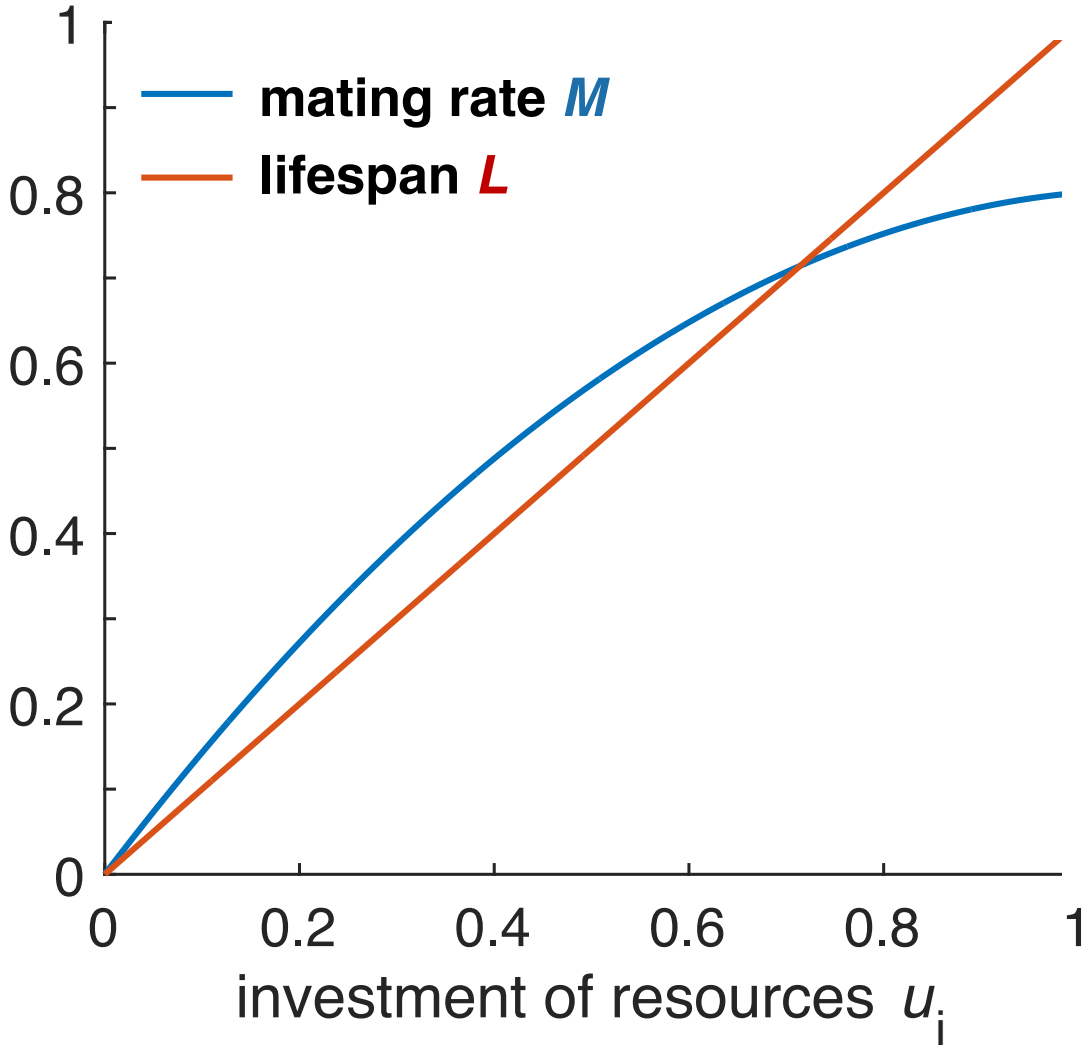
Unless $L(u_L)$ is accelerating, optimal investment in mating rate (u_M), and hence **signal strength, strictly increases with quality** (R).


mating rate M
lifespan L
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
investment of resources u_i


attainable trait combinations for
low
medium
high
quality males
mating rate M
0
0.2
0.4
0.6
0.8
1
lifespan L


mating rate M
lifespan L
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
investment of resources u_i


fitness isoclines
attainable trait combinations for
low
medium
high
quality males
mating rate M
0
0.2
0.4
0.6
0.8
1
lifespan L


mating rate M
lifespan L
1
0.8
0.6
0.4
0.2
0
0
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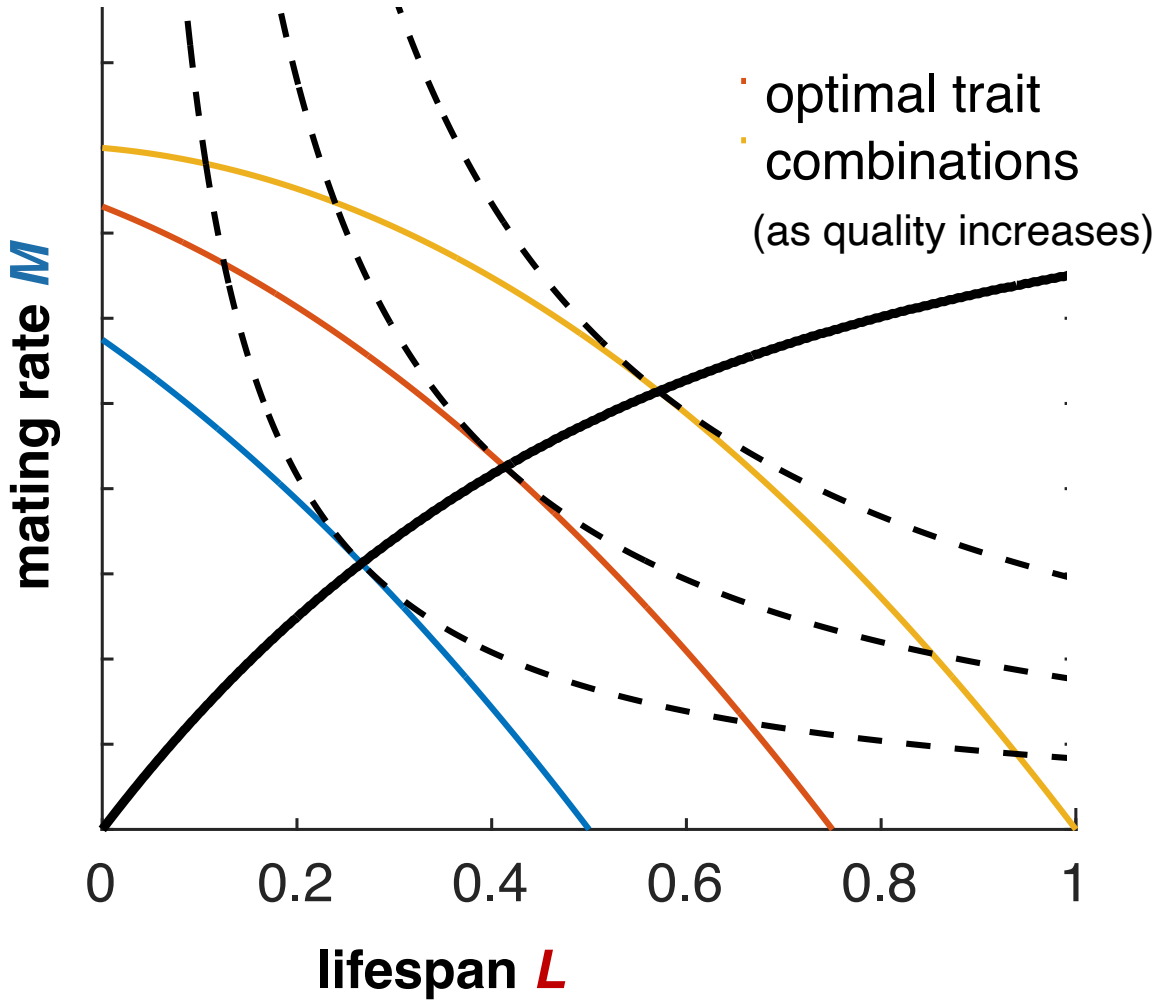
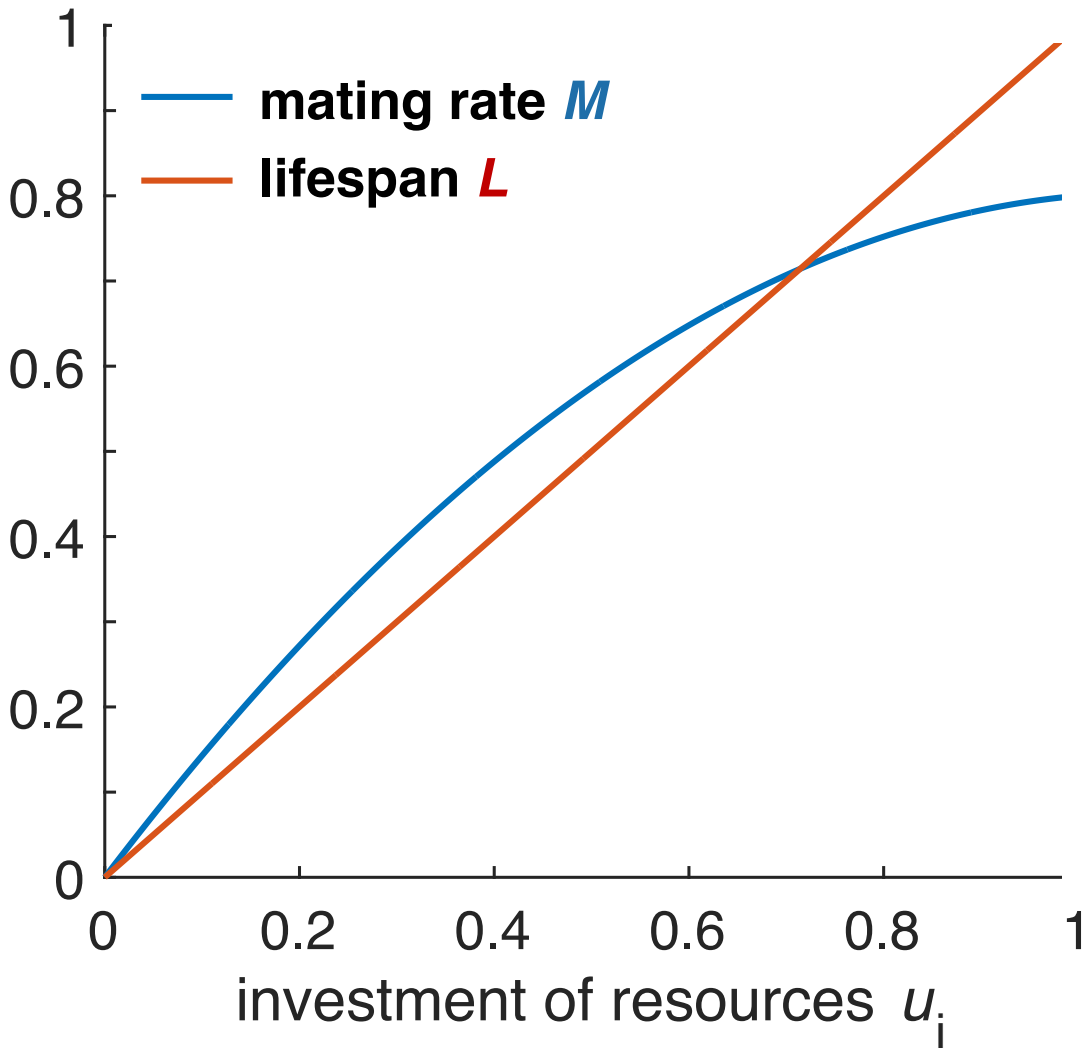
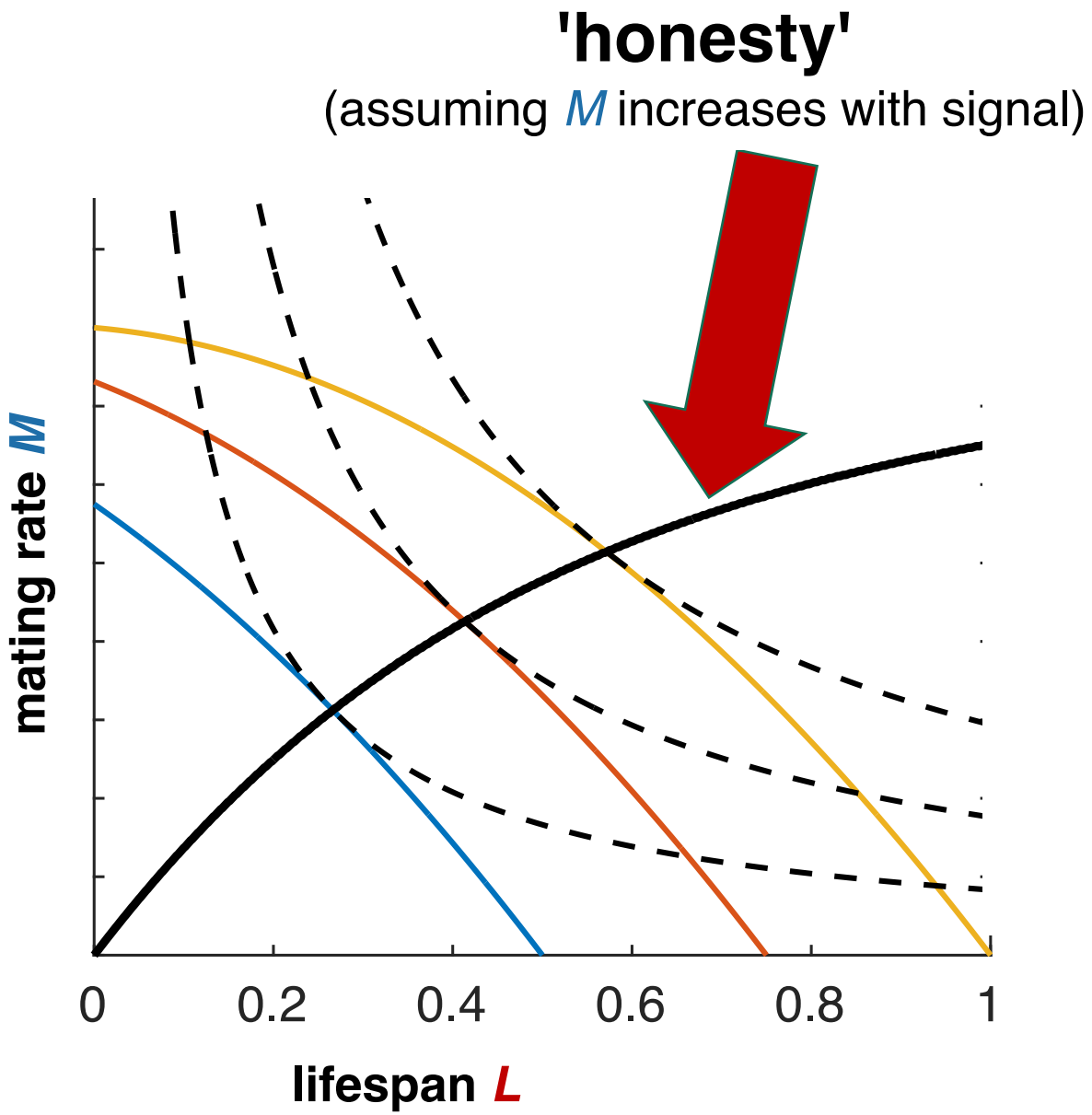
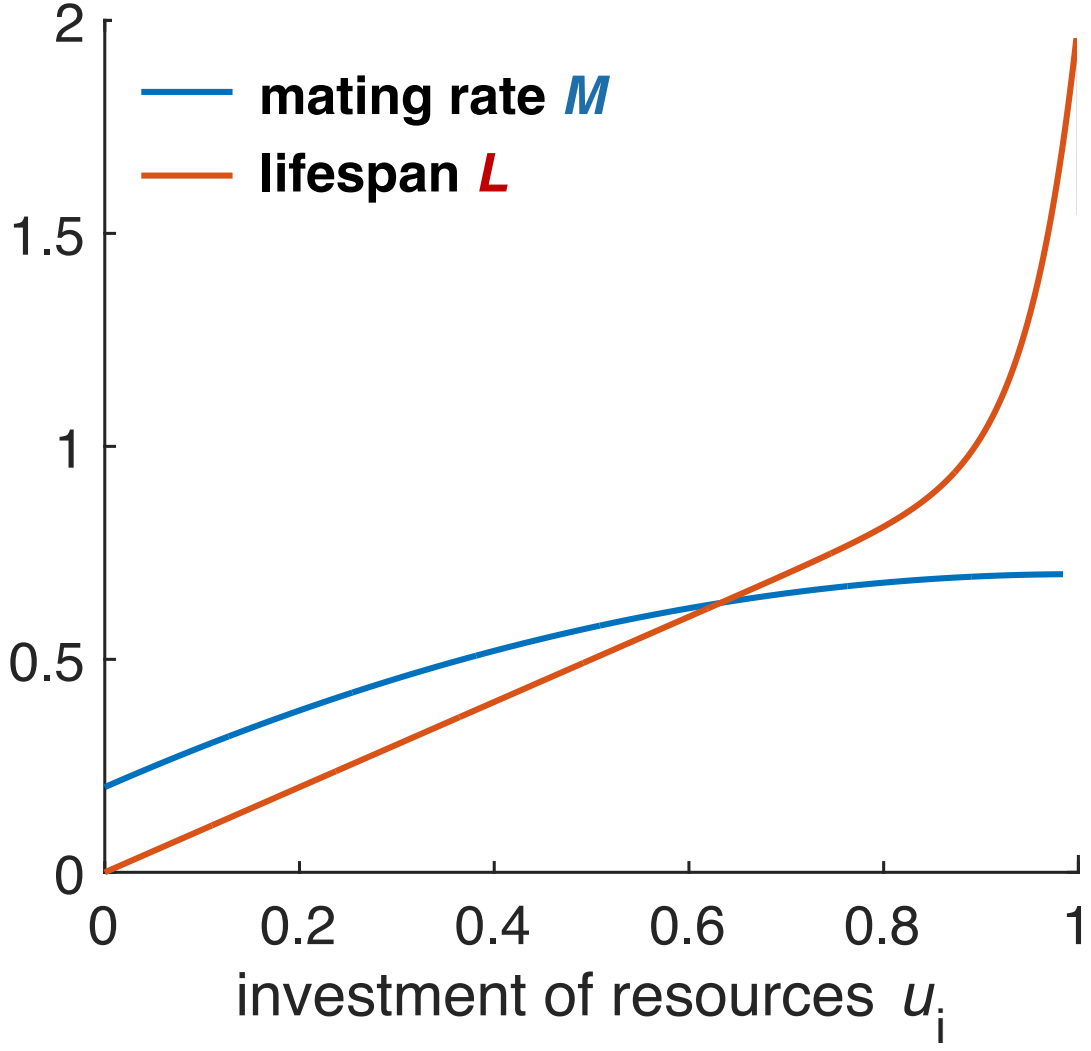
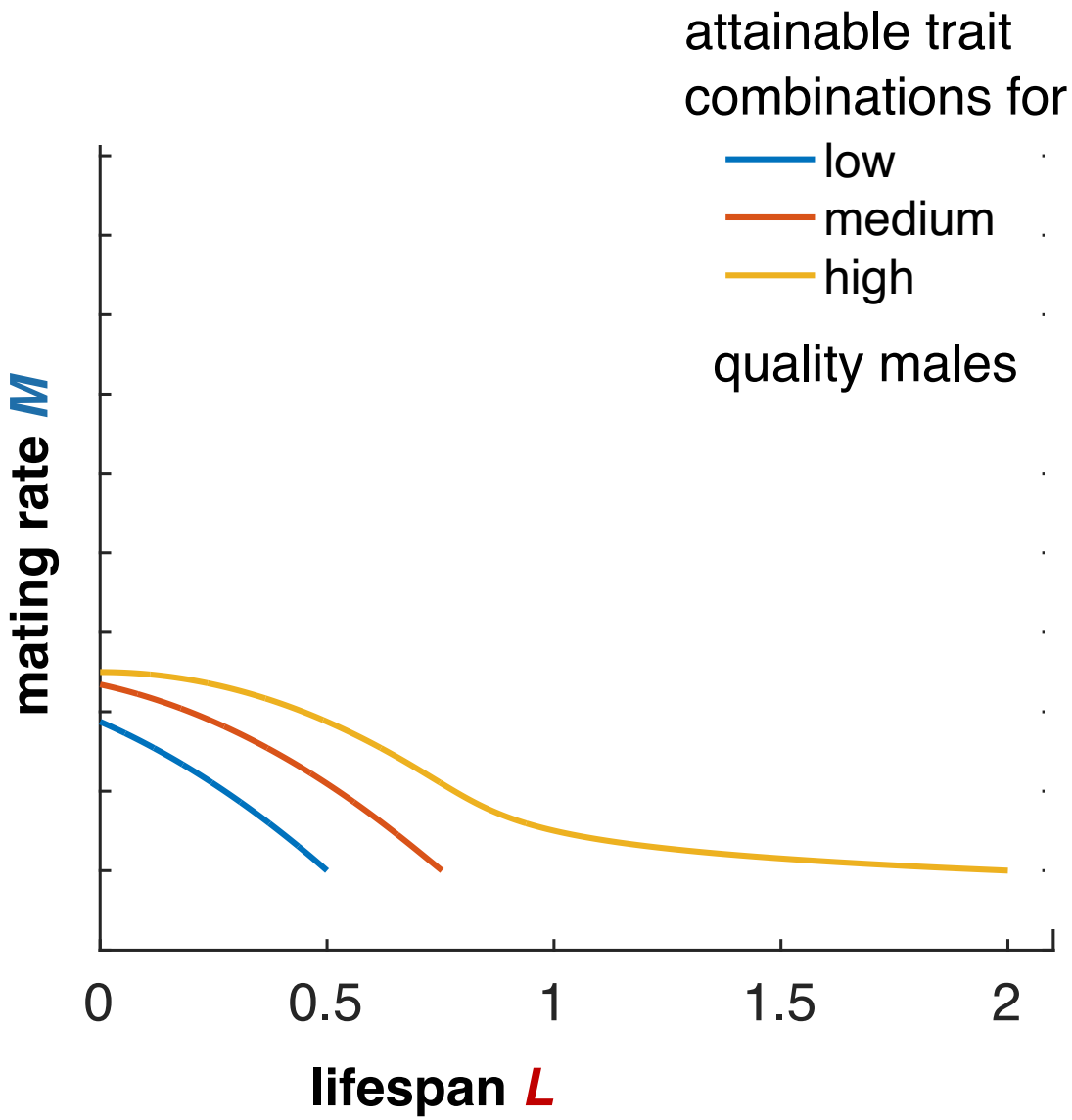
0.6
0.8
1
investment of resources u_i

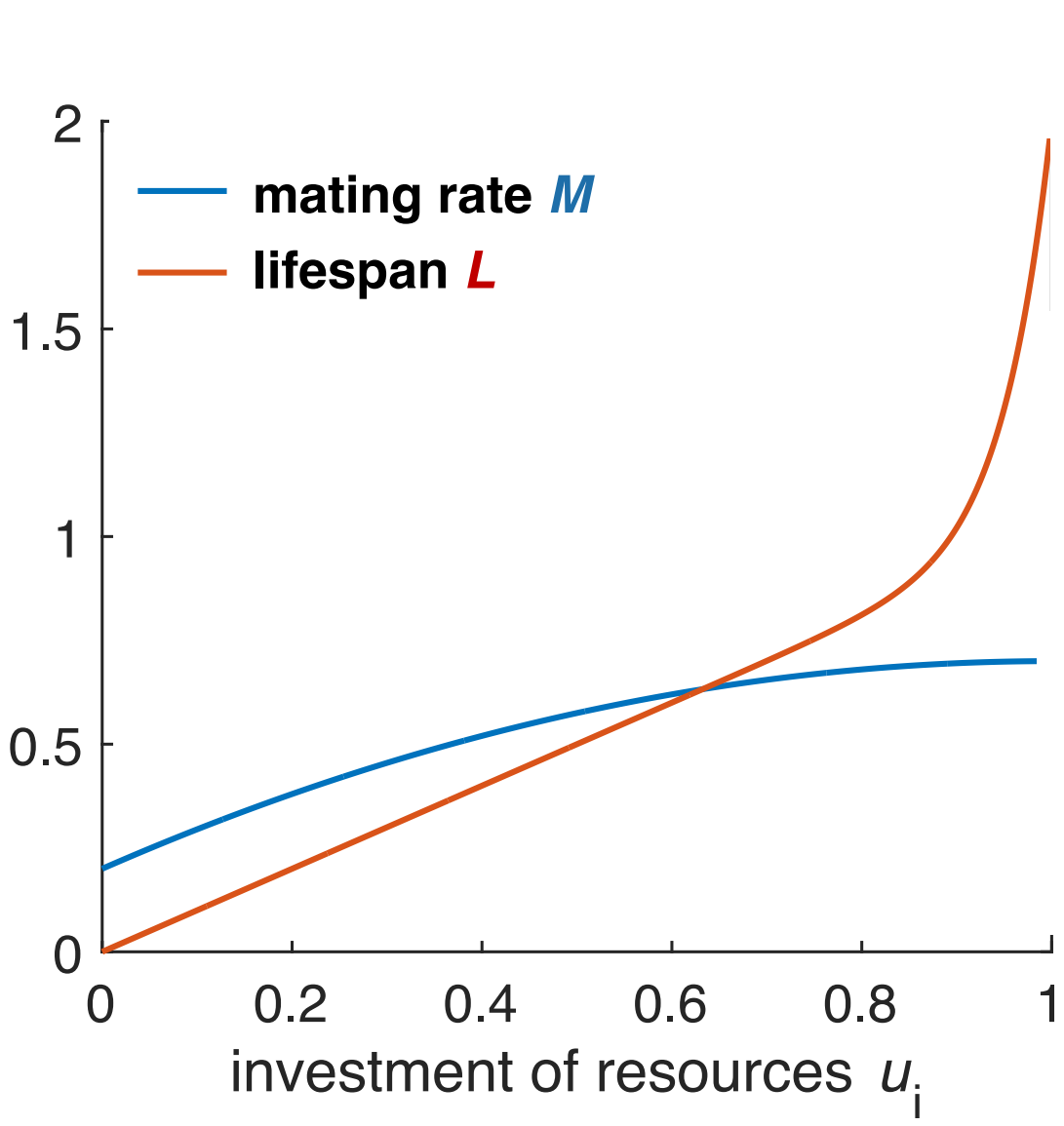

optimal trait
combinations
(as quality increases)
mating rate M
0
0.2
0.4
0.6
0.8
1
lifespan L

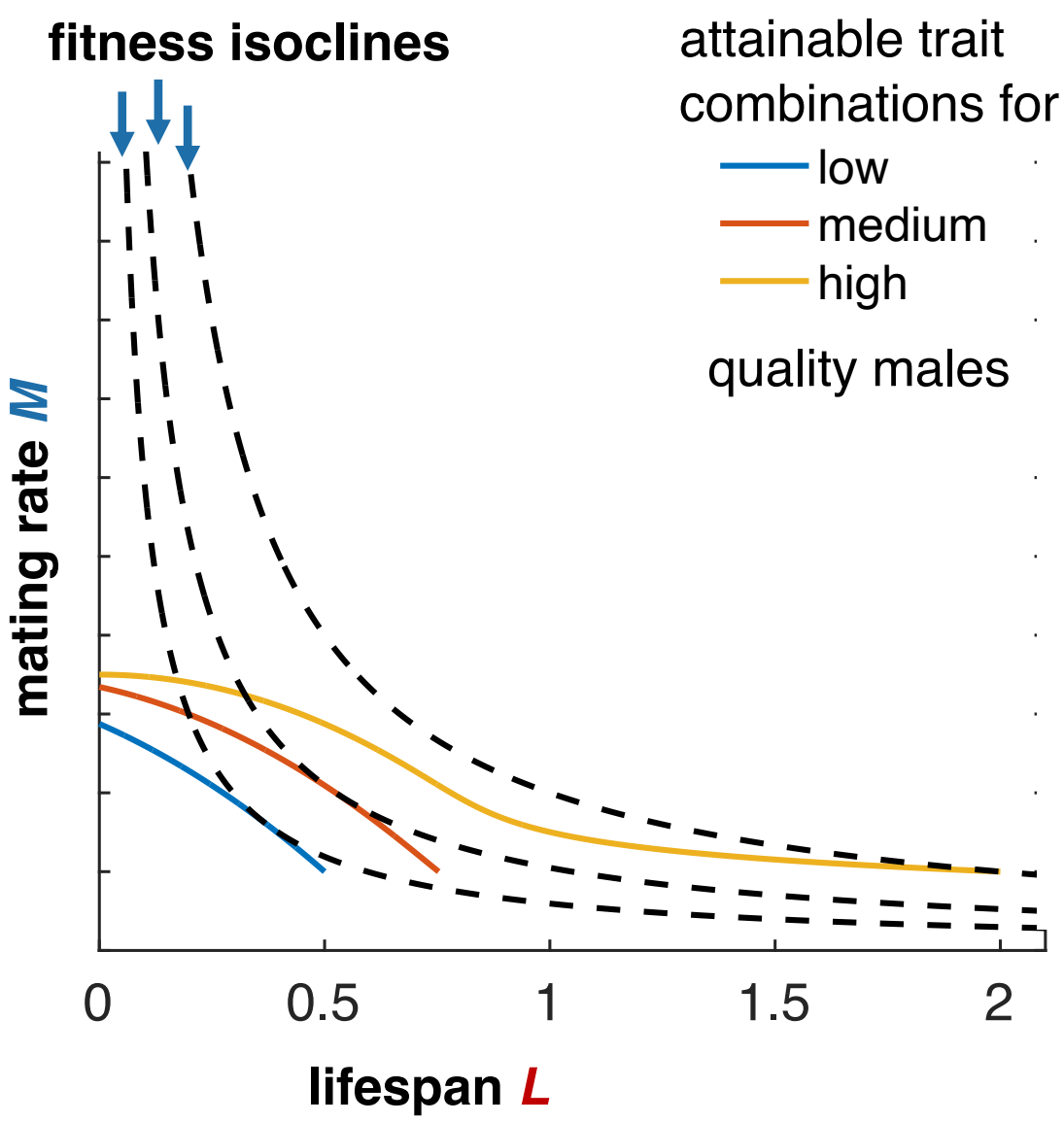

mating rate M
lifespan L
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
investment of resources u_i


'honesty'
(assuming M increases with signal)
mating rate M
0
0.2
0.4
0.6
0.8
1
lifespan L


mating rate M
lifespan L
2
1.5
1
0.5
0
0
0.2
0.4
0.6
0.8
1
investment of resources u_i


attainable trait combinations for
low
medium
high
quality males
mating rate M
0
0.5
1
1.5
2
lifespan L


mating rate M
lifespan L
2
1.5
1
0.5
0
0
0.2
0.4
0.6
0.8
1
investment of resources u_i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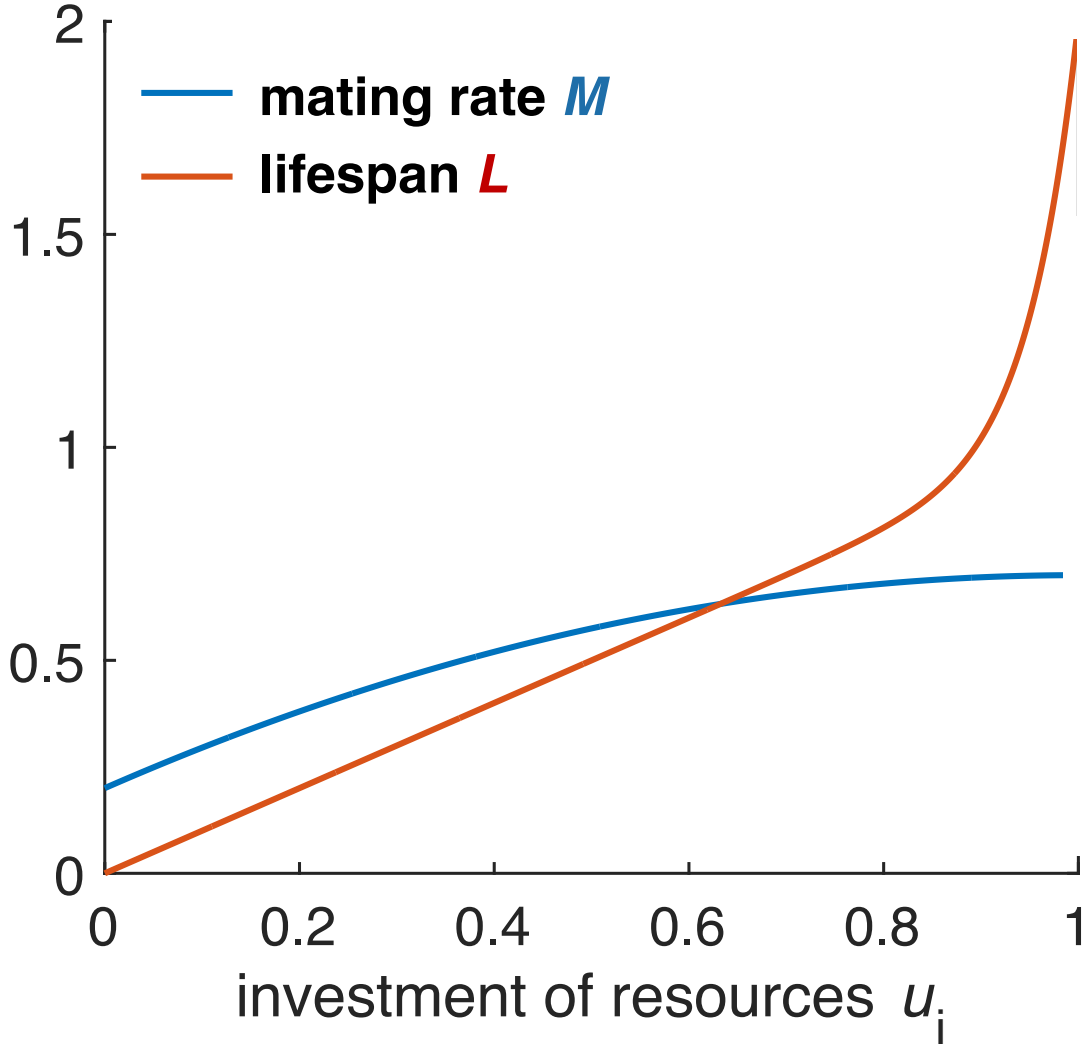
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0.6
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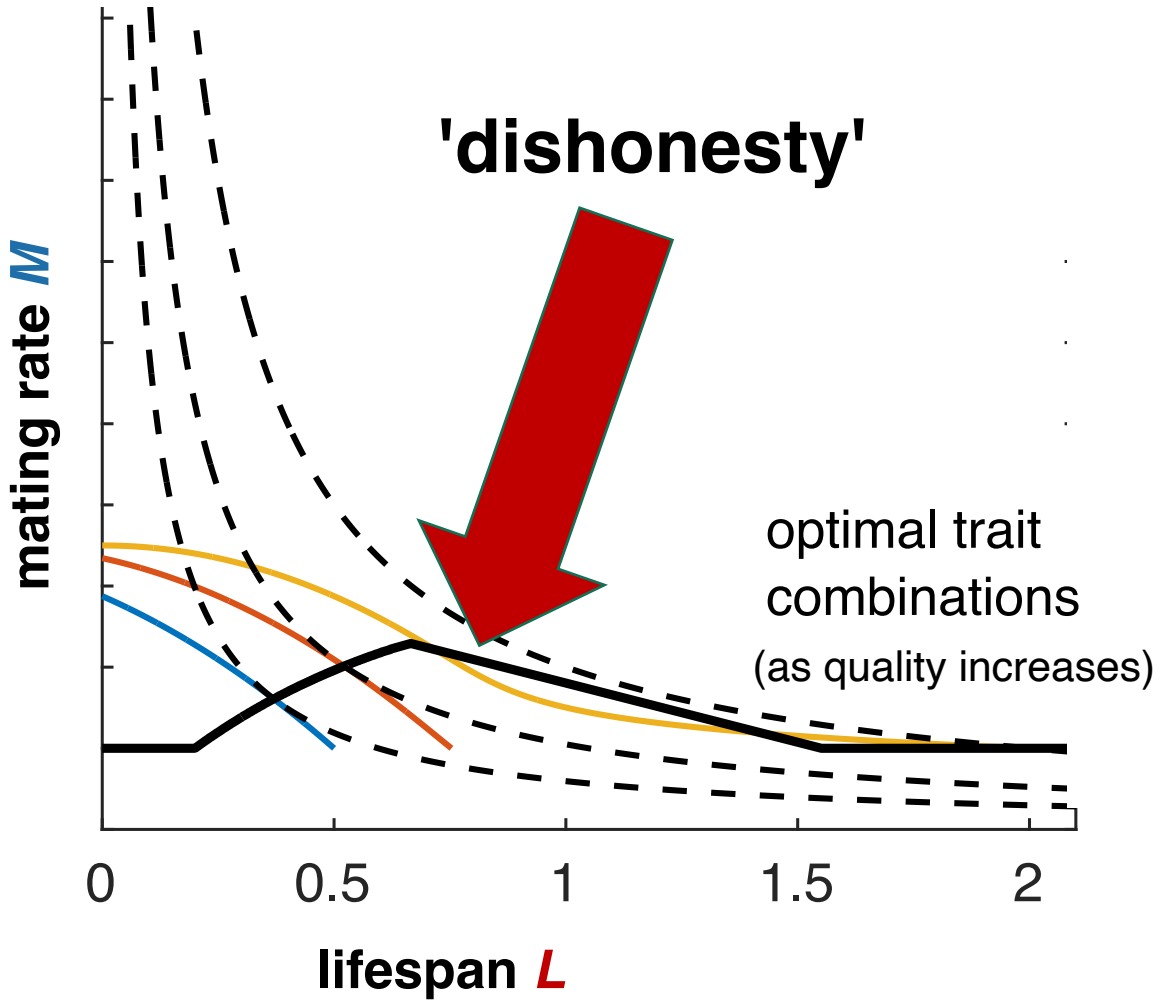
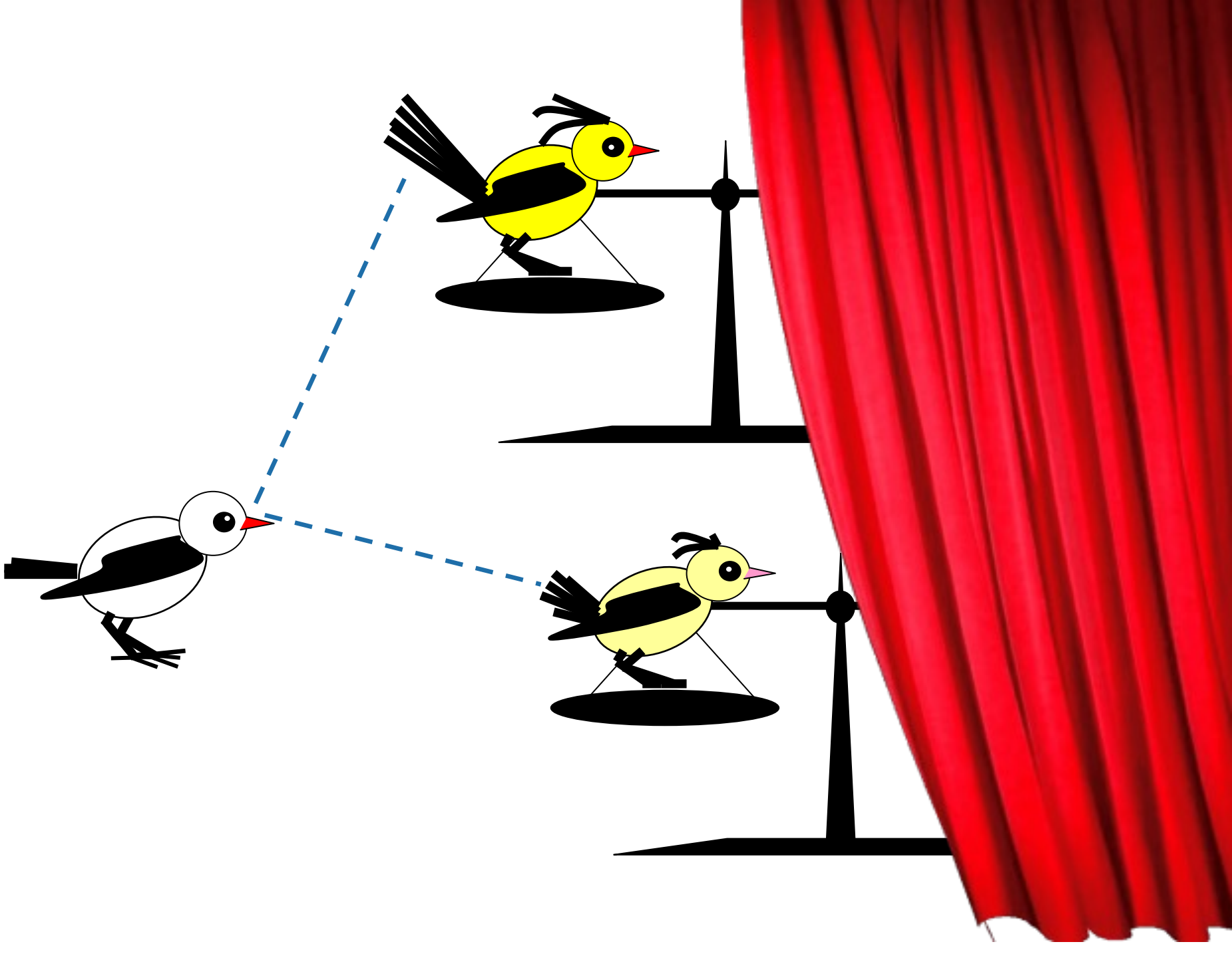
1
investment of resources u_i


'dishonesty'
optimal trait combinations
(as quality increases)
mating rate M
0
0.5
1
1.5
2
lifespan L


10 kg


5 kg



'big house, big car' effect

Metaphorical explanation for positive correlations between life-history traits involved in trade-offs

'big house, big car' effect

“if the budget is fixed, people spending more on housing should spend less on cars. In fact, the amount of expendable income is variable, and in many situations positive correlations are observed between the per-family expenses on housing and cars”

van Noordwijk & de Jong 1986

Take-home message:

Signal 'honesty' can arise naturally from a need to 'balance' investments.

Jonathan (Jono) Henshaw