Anisogamy selects for male-biased care in self-consistent games with synchronous matings

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Parental investment hypothesis

- Proposed by Trivers (1972) to explain prevalence of female-care across taxa
  - Although there is diversity (e.g. biparental care in most birds, male-care in fish and frogs, no care in a number of taxa)
- 'Female argument': Due to anisogamy, female has more to lose than the male if the zygote fails; so she invests more in care
- Issues: Sunk cost fallacy (Dawkins and Carlisle 1976): need prospective rather than retrospective analyses
- 'Male argument': Male care decreases his chances of inseminating other females, so he should rather compete for matings
- Issues: Why not care when competition for mates is costly (Kokko and Jennions 2008)

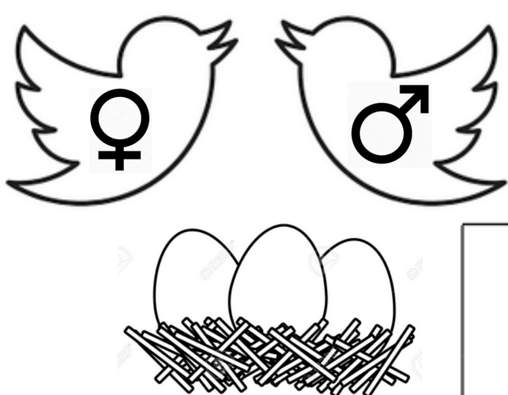
Maynard Smith's model-2 (1977)

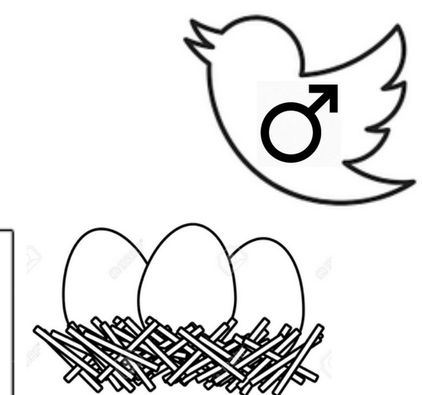
- Prospective analysis
- Female who deserts lays additional eggs ($W_d > W_c$), male who deserts gains additional matings (with probability p), offspring survival increases with number of parents caring ($V_2 > V_1 > V_0$)

Strategies	**Female cares** $(1 - f_d)$	**Female deserts** (f_d)
Male cares $(1 - m_d)$	$(W_c V_2, W_c V_2)$	$(W_d V_1, W_d V_1)$
Male deserts (m_d)	$(W_c V_1 (1 + p), W_c V_1)$	$(W_d V_0 (1 + p), W_d V_0)$

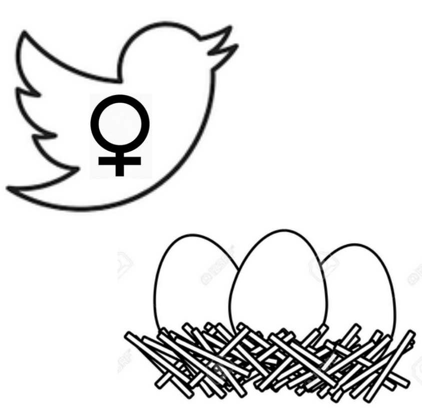
Maynard Smith's model-2 (1977)

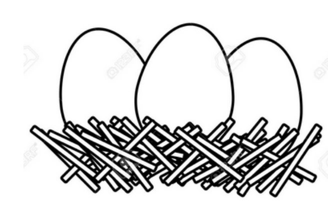
All 4 patterns of ESS possible based on parameters





Strategies	Female cares $(1-f_d)$	Female deserts (f_d)
Male cares $(1-m_d)$	(W_cV_2, W_cV_2)	(W_dV_1, W_dV_1)
Male deserts (m_d)	$(W_cV_1(1+p), W_cV_1)$	$(W_dV_0(1+p), W_dV_0)$





But the game is not self-consistent! (Wade & Shuster 2002)

Aim of this study

- To formulate multiple self-consistent versions of Maynard Smith's game-2 that incorporate:
- Expected consequences of anisogamy for gamete production and their trade-offs with parental investment, and for patterns of mate limitation:
    - C1: Expensive eggs → Total eggs produced by a female limited
    - C2: Cheap sperm → Sperm production per se not expected to constrain the number of matings for a male
    - C3: Expensive eggs → Number of eggs produced trades off with costly behaviours such as parental care
    - C4: Cheap sperm → Sperm production is less likely to trade-off with costly behaviours such as parental care
    - C5: Females need not be mate limited, but males are more likely to be

Additional factors

- Mating-caring trade-off for males:
  - Assumed by Maynard Smith (1977) and included in many of our models
  - C4 implies this trade-off need not exist/ can be weaker (empirical examples in Stiver and Alonzo 2009): explored in some of our models
  - Fromhage and Jennions (2016) include trade-off between parental care and investment into costly competition; we do not model co-evolution with costly competitive traits
- Not included in our models: investment in costly competitive traits, sexual selection, partial parentage
  - All of these could bias ESS towards more female care (Queller 1997, Kokko and Jennions 2008, Fromhage and Jennions 2016)

Model assumptions

- Additional eggs laid by a deserting female (W_d-W_c) are laid as a separate clutch requiring additional mating: source of mating opportunities for males

- Analytical models assume matings in the population are synchronous, hence two rounds of mating per breeding season

- No mortality differences between sexes or strategies, hence we assume each generation consists of a single breeding season.

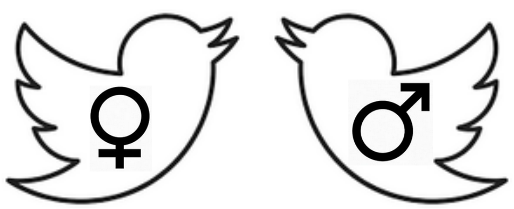
Game-1: baseline

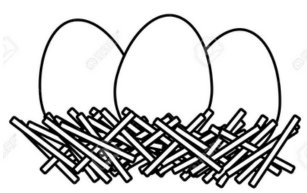
- Only deserting males remate; no limit on the number of rematings
- Expected number of rematings per deserting male = f_d/m_d

Strategies	**Female cares** $(1-f_d)$	**Female deserts** (f_d)
Male cares $(1-m_d)$	$(W_cV_2,$ $W_cV_2)$	$(W_cV_1,$ $W_cV_1+(W_d-W_c)V_0)$
Male deserts (m_d)	$(W_cV_1+f_d/m_d(W_d-W_c)V_0,$ $W_cV_1)$	$(W_cV_0+f_d/m_d(W_d-W_c)V_0,$ $W_cV_0+(W_d-W_c)V_0)$

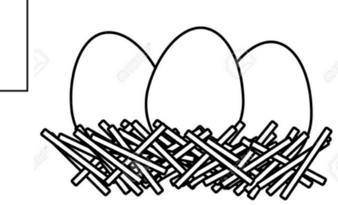
Game-1: baseline

- ESS are symmetric: both sexes desert or care with equal probability





Strategies	**Female cares** $(1-f_d)$	**Female deserts** (f_d)
Male cares $(1-m_d)$	$(W_cV_2,$ $W_cV_2)$	$(W_cV_1,$ $W_cV_1+(W_d-W_c)V_0)$
Male deserts (m_d)	$(W_cV_1+f_d/m_d(W_d-W_c)V_0,$ $W_cV_1)$	$(W_cV_0+f_d/m_d(W_d-W_c)V_0,$ $W_cV_0+(W_d-W_c)V_0)$



Game-2: caring males can remate

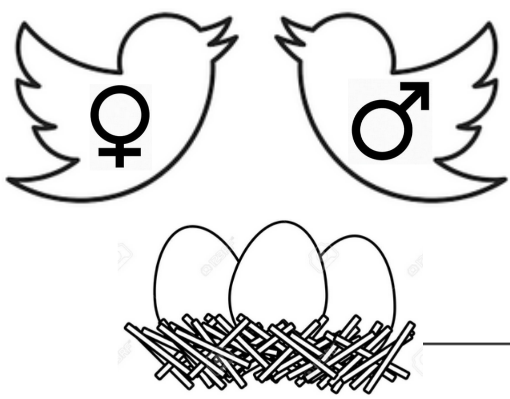
Weaker mating-caring trade-off for males → caring males can also remate (with lower probability of remating)

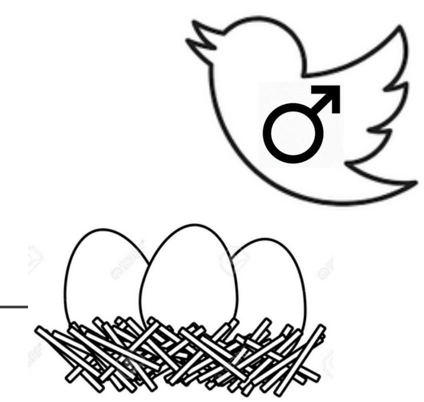
Remating advantage of deserting males is given by α (α=1 corresponds to remating only by deserting males as in Game-1)

Strategies	Female cares $(1-f_d)$	Female deserts (f_d)
Male cares $(1-m_d)$	$(W_cV_2 + \frac{1-\alpha}{(1-\alpha)(1-m_d)+m_d} f_d(W_d - W_c)V_0,$ $W_cV_2)$	$(W_cV_1 + \frac{1-\alpha}{(1-\alpha)(1-m_d)+m_d} f_d(W_d - W_c)V_0,$ $W_cV_1 + (W_d - W_c)V_0)$
Male deserts (m_d)	$(W_cV_1 + \frac{1}{(1-\alpha)(1-m_d)+m_d} f_d(W_d - W_c)V_0,$ $W_cV_1)$	$(W_cV_0 + \frac{1}{(1-\alpha)(1-m_d)+m_d} f_d(W_d - W_c)V_0,$ $W_cV_0 + (W_d - W_c)V_0)$

Game-2: caring males can remate

Male-biased care ESS also possible in this game, apart from symmetric ESS





Strategies	Female cares $(1-f_d)$	Female deserts (f_d)
Male cares $(1-m_d)$	$(W_cV_2 + \frac{1-\alpha}{(1-\alpha)(1-m_d)+m_d} f_d(W_d - W_c)V_0,$ $W_cV_2)$	$(W_cV_1 + \frac{1-\alpha}{(1-\alpha)(1-m_d)+m_d} f_d(W_d - W_c)V_0,$ $W_cV_1 + (W_d - W_c)V_0)$
Male deserts (m_d)	$(W_cV_1 + \frac{1}{(1-\alpha)(1-m_d)+m_d} f_d(W_d - W_c)V_0,$ $W_cV_1)$	$(W_cV_0 + \frac{1}{(1-\alpha)(1-m_d)+m_d} f_d(W_d - W_c)V_0,$ $W_cV_0 + (W_d - W_c)V_0)$

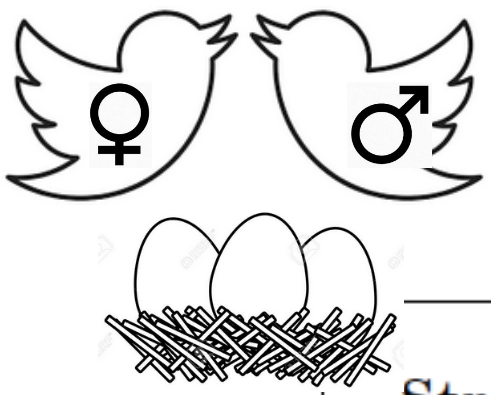
Game-3

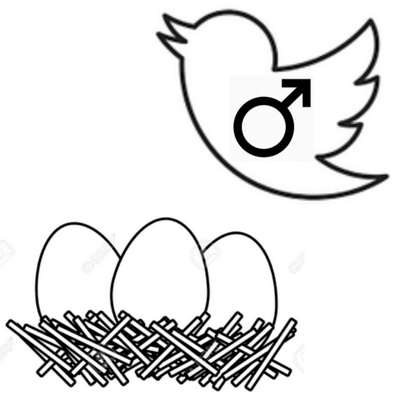
Female control over the number of eggs → Deserting females can lay more eggs in the first clutch ($W_0 > W_c$; decreasing the number of eggs in the second)

Strategies	Female cares $(1 - f_d)$	Female deserts (f_d)
Male cares $(1 - m_d)$	$(W_c V_2, W_c V_2)$	$(W_0 V_1, W_0 V_1 + (W_d - W_0) V_0)$
Male deserts (m_d)	$(W_c V_1 + f_d/m_d (W_d - W_0) V_0, W_c V_1)$	$(W_0 V_0 + f_d/m_d (W_d - W_0) V_0, W_0 V_0 + (W_d - W_0) V_0)$

Game-3

Male-biased care ESS, apart from symmetric ESS





Strategies	Female cares $(1-f_d)$	Female deserts (f_d)
Male cares $(1-m_d)$	$(W_cV_2,$ $W_cV_2)$	$(W_0V_1,$ $W_0V_1+(W_d-W_0)V_0)$
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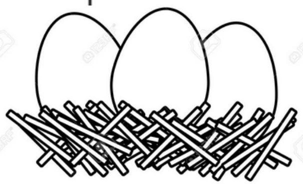


Analytical models: Results

- All the analytical models yield either symmetric sex roles or male-biased care ESS
- All of them also assume that matings in the population are synchronous within each of the two mating rounds
- Can relax that assumption and model asynchrony of matings with agent based models

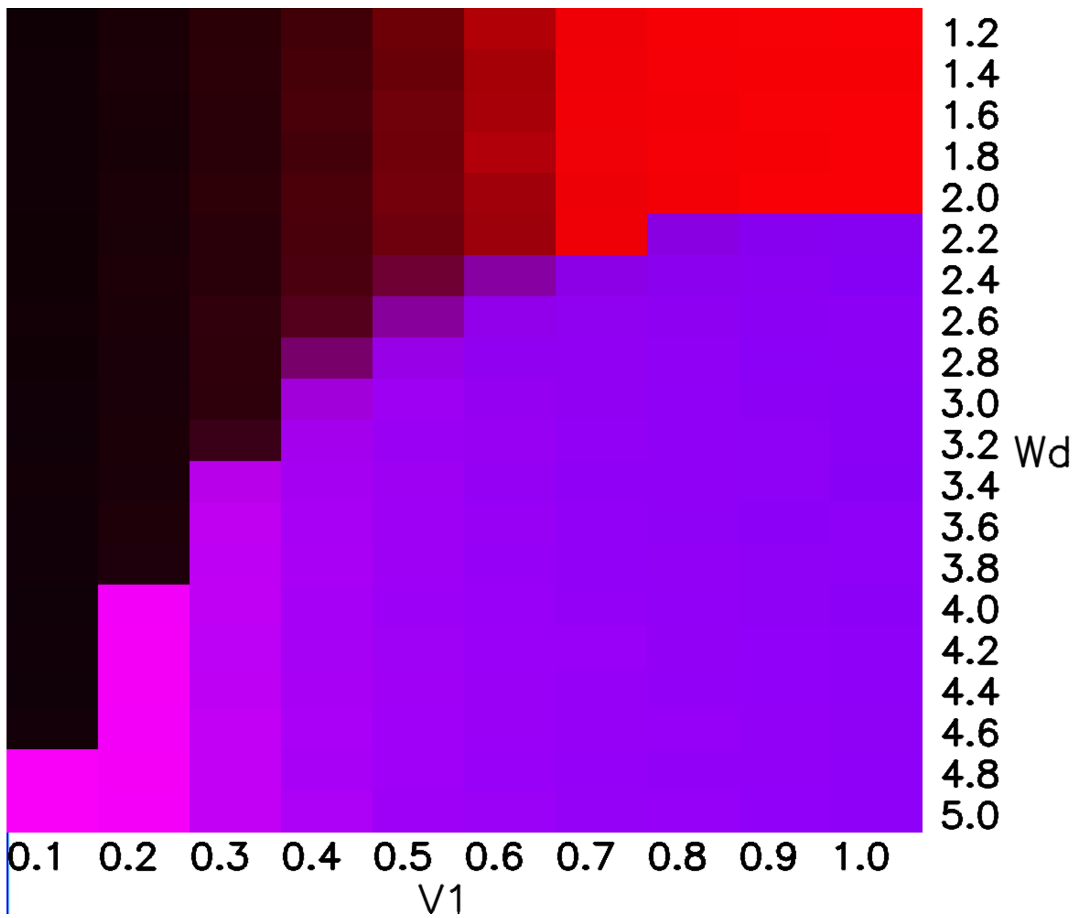
Agent based simulations

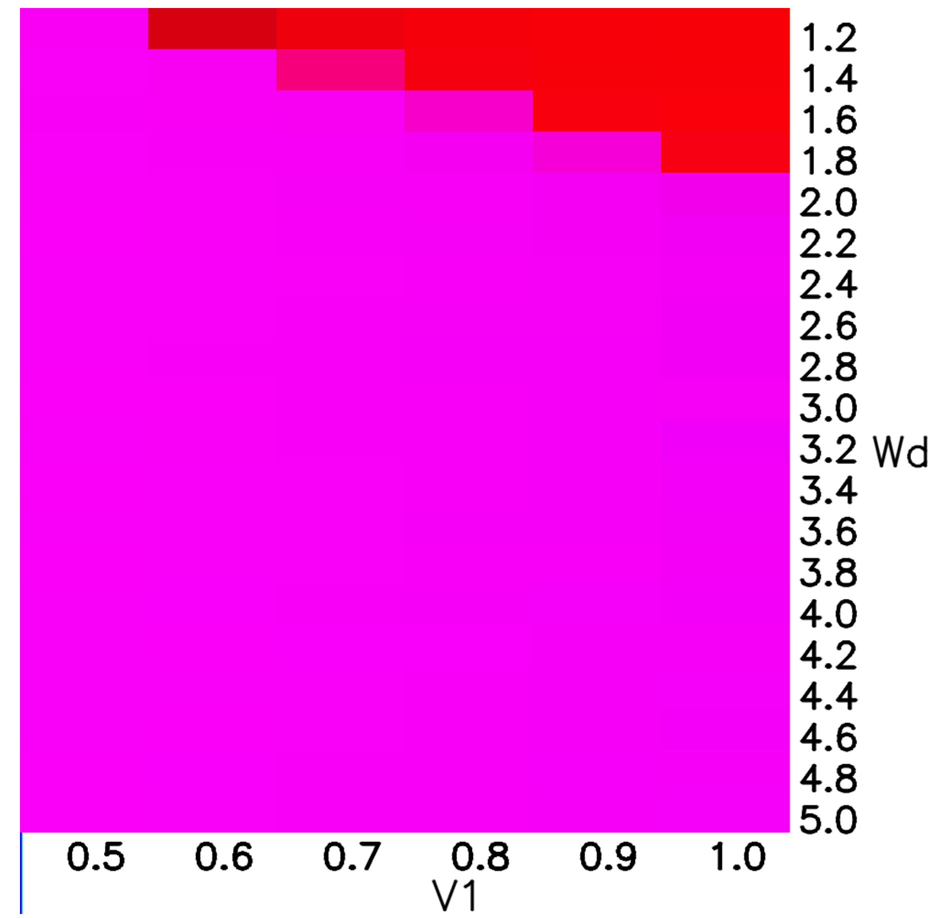
- With asynchrony of matings within the population, deserting males could also remate with unmated females
- Simulations that reflect the rules of games 1-3 (algorithm in Section 2.1, SI)
- m_d and f_d evolve: inherited in the next generation in proportion to fitness in the previous generation

Agent-based simulations- 1 (baseline)

$W_c = 1$
$V_2 = 1$
kept constant

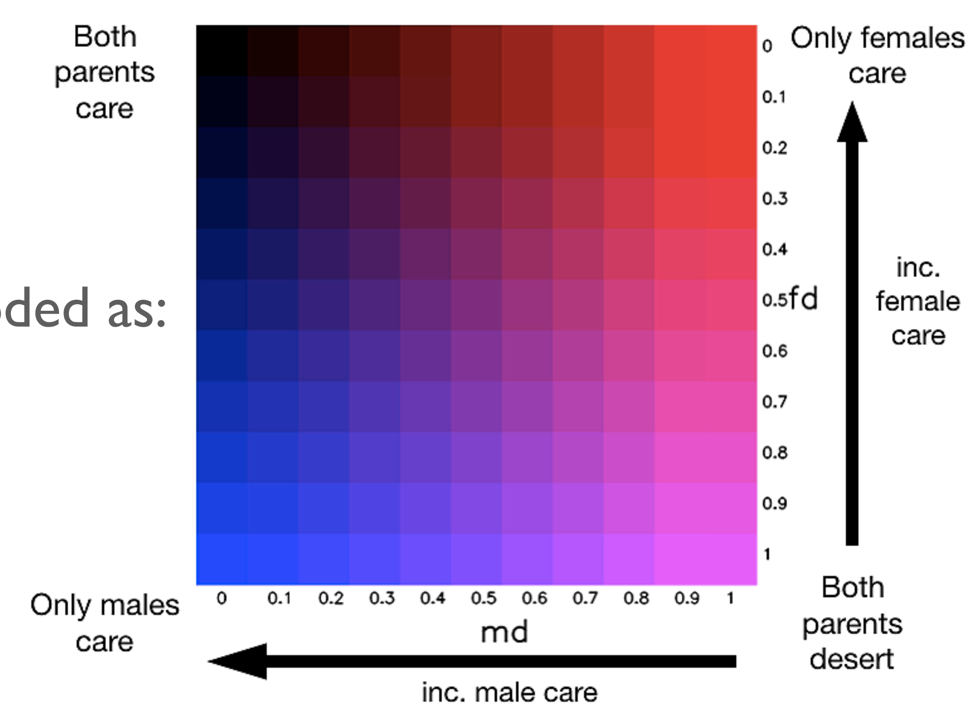
$V_0 = 0.1$





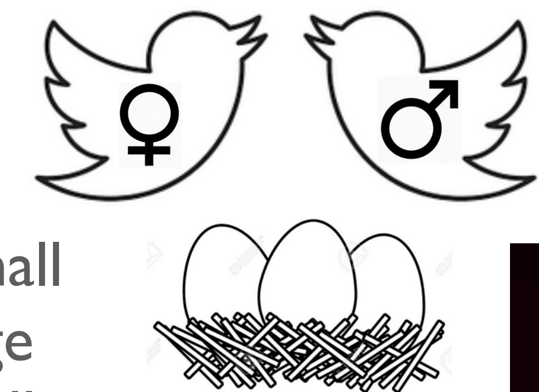
$V_0 = 0.5$

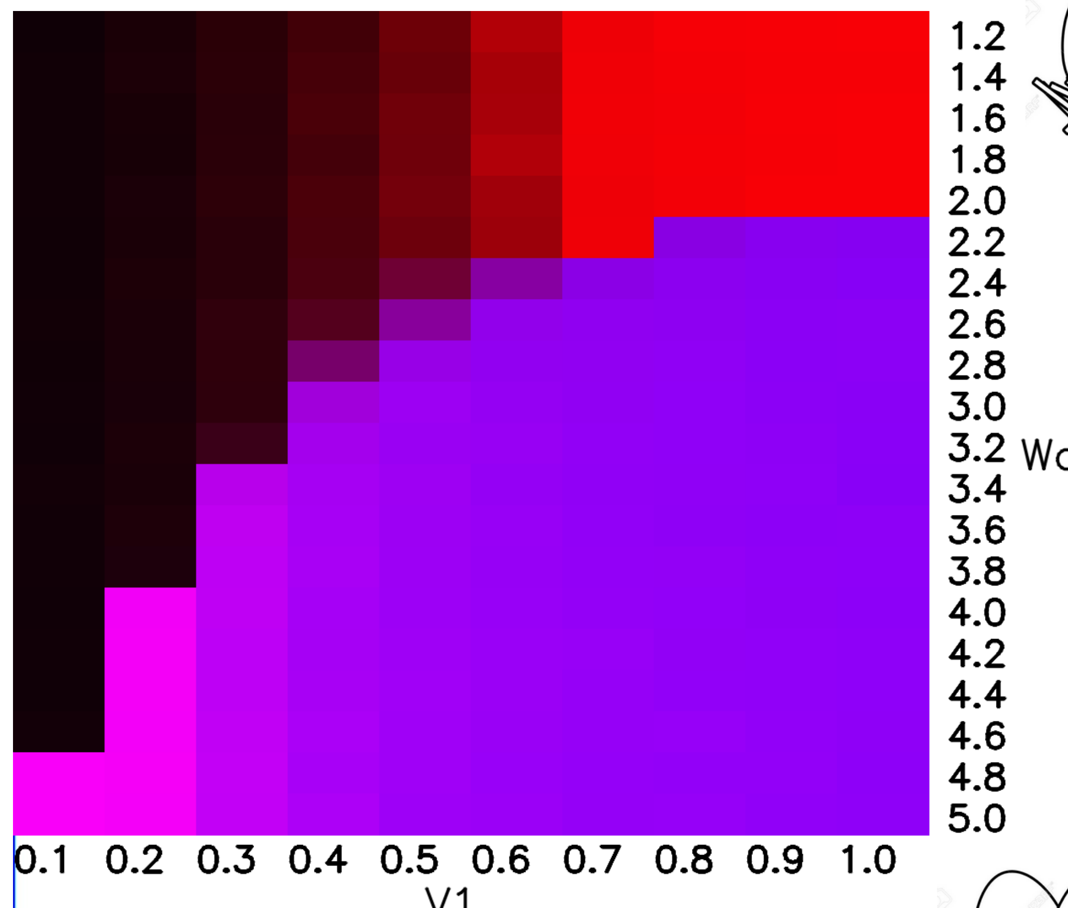
ESS colour-coded as:

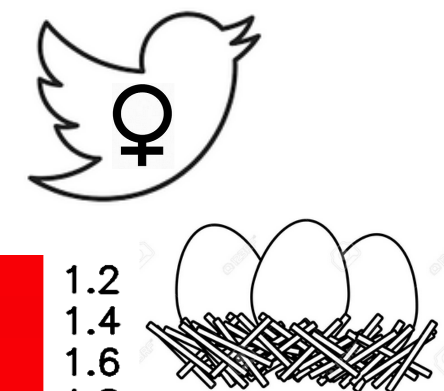


Agent-based simulations- 1 (baseline)

$W_d - W_c$ small
$V_2 - V_1$ large
$V_1 - V_0$ small

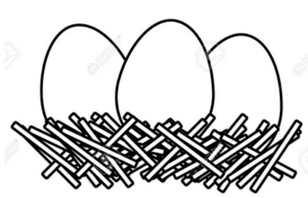


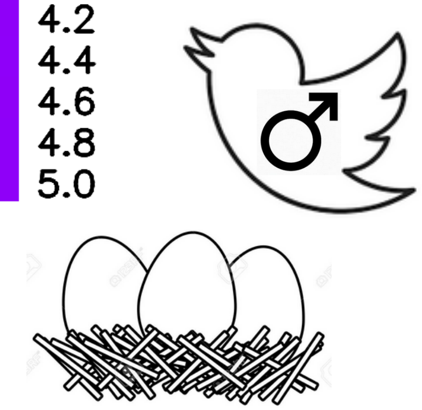




$W_d - W_c$ small
$V_2 - V_1$ small
$V_1 - V_0$ large

$W_d - W_c$ large
$V_1 - V_0$ small





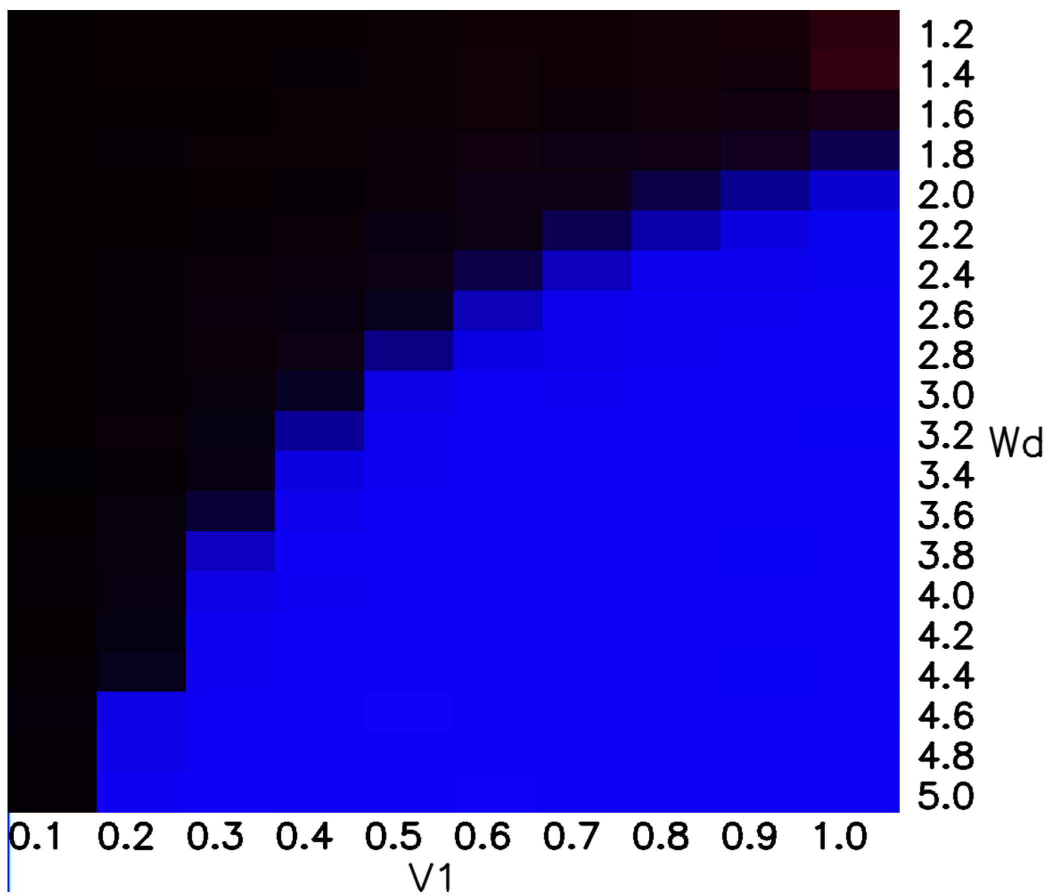
$W_d - W_c$ large
$V_1 - V_0$ large

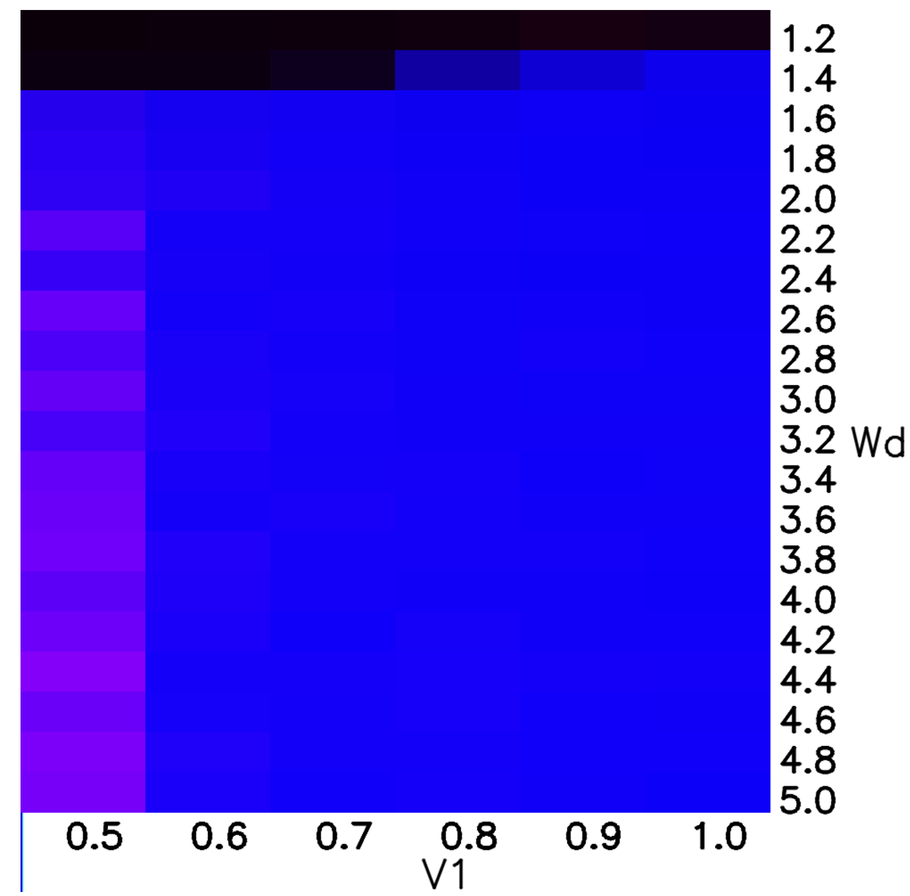
All 4 kinds of ESS possible based on parameters; also depends on initial conditions (Sec 2.3)

Agent-based simulations- 2 (caring males remate and $\alpha = 0$)

$W_c = 1$
$V_2 = 1$
kept constant

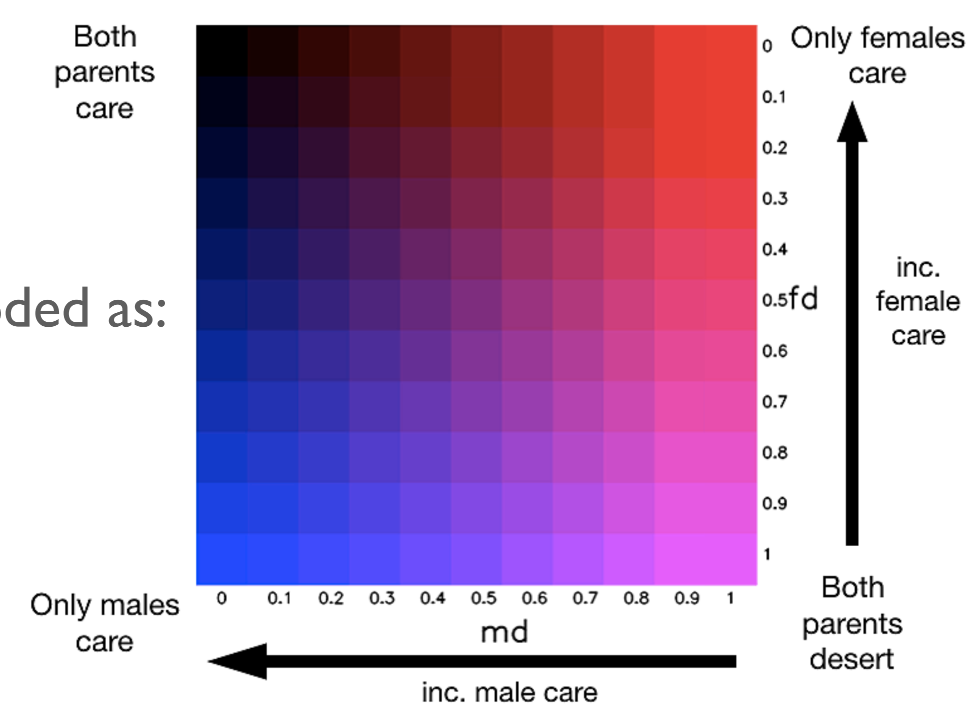
$V_0 = 0.1$





$V_0 = 0.5$

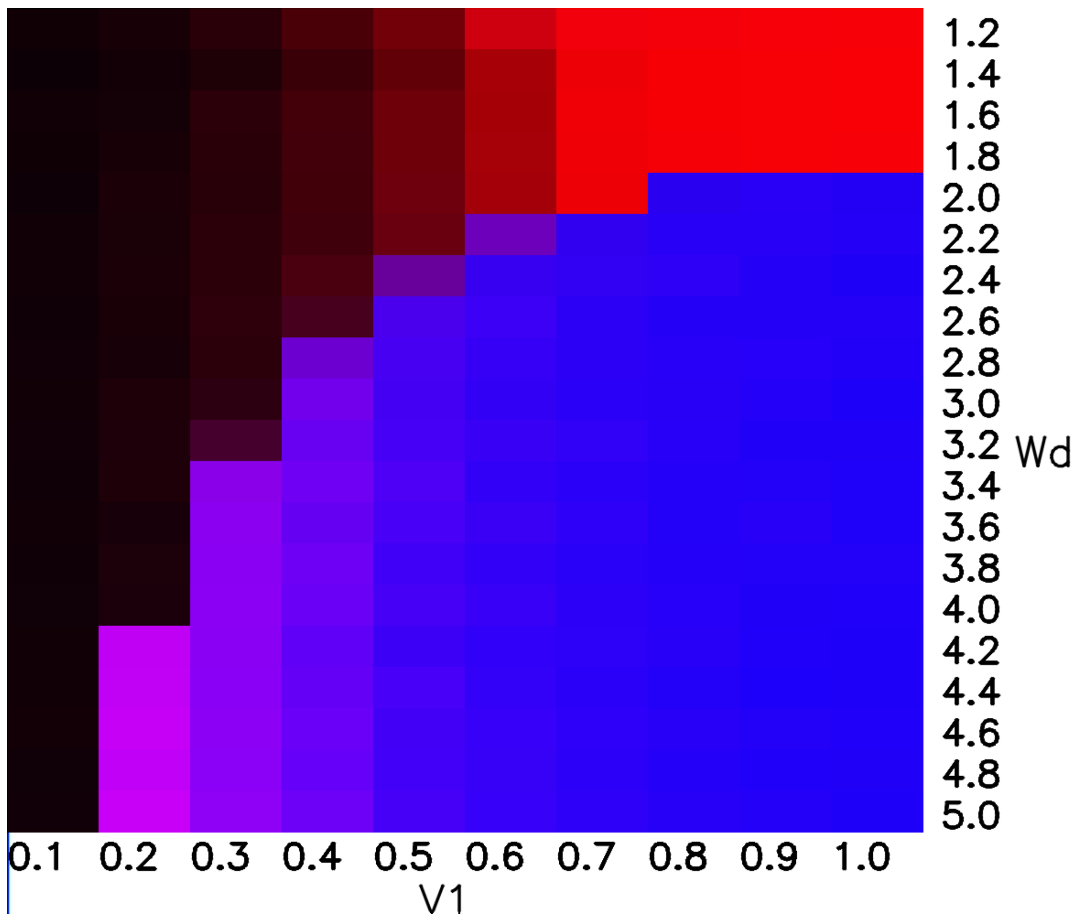
ESS colour-coded as:

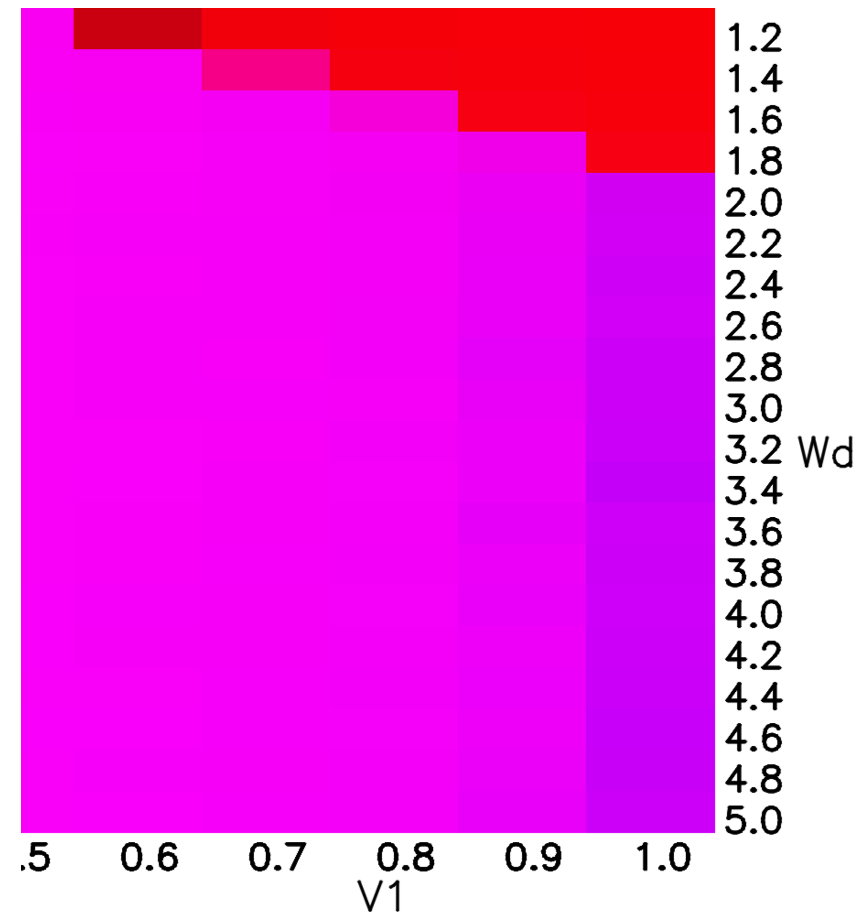


Agent-based simulations- 3 ($W_0 = W_d$)

$W_c = 1$
$V_2 = 1$
kept constant

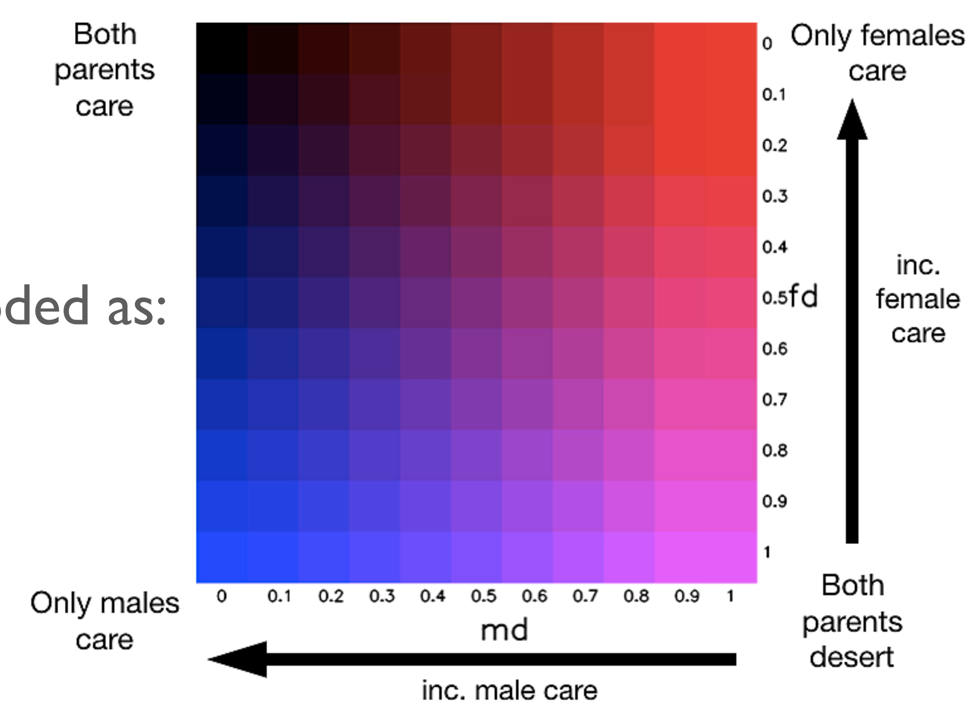
$V_0 = 0.1$





$V_0 = 0.5$

ESS colour-coded as:



Agent based simulations: Results

- All patterns of ESS (including female-only care) possible when matings in the population are asynchronous
  - These results qualitatively similar to continuous-time models of Yamamura and Tsuji (1993) and Ramsey (2009, 2010)
- When matings in the population are synchronous, ESS are either symmetric or male-biased care (Sec 2.4 SI)
- As caring males become more likely to remate, male care becomes more likely (see Sec 2.5 SI)
- As W_0 increases, male care increases and female care decreases (see Sec 2.8 SI)
- Frequency-dependent selection on males and co-evolution of male and female strategies in all the models

Implications

- Extent of synchrony of matings in the population is important for the ESS selected
- Male-biased care ESS in the analytical models and ABS (despite incorporation of multiple consequences of anisogamy) refute the generality of the parental investment hypothesis
- Incorporating consequences of anisogamy for gamete production and their trade-offs with parental care (eg C4) can select for more male care
- No evidence for the female argument of parental investment hypothesis
- Parentage and sexual selection considerations we do not include: could be important to explain prevalence of female-care in nature

Mating-caring trade-off and male argument

- Trivers posits that the trade-off between mating and caring for males selects for them to provide less care and compete over matings more
- Mating-caring trade-off for males incorporated in all our models (strongly so in games 1 & 3): insufficient to select for female-care, esp due to frequency-dependent selection
- Male argument may work when additionally there is trade-off between parental investment and costly competition for mates (Fromhage and Jennions 2016)
- But cheap sperm also implies mating-caring trade-off could be weak or non-existent: selects for male-care ESS
- Further, there could be a positive relationship between mating and caring (eg due to sexual selection for care): favours male-care ESS even more strongly (Alonzo 2012)
- The particular relationship between mating and caring may depend on mating system and evolutionary history (Stiver & Alonzo 2009)

Empirical implications of male-care ESS

- Male-biased care selected in our models due to:
  - Weaker trade-off between mating and caring: may select for paternal care in fish (Gross & Sargent 1985) and birds (Wesolowski 1994)
  - Females may lay more eggs when freed from caring: may select for paternal care in birds (Van Rhijn 1990, Wesolowski 1994, 2004)
  - Both may play a crucial role in biasing sex roles, esp when matings synchronous
- Ancestral transitions in both fish and birds may have been from no care to male-care (Balshine 2012, Ah-King et al 2005, Wesolowski 2004)
  - Empirically refute the generality of parental investment hypothesis
  - Our models could provide possible explanations