Intrafamily and intragenomic conflicts in human warfare

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Introduction

- Recent multidisciplinary interest in ancient human warfare, i.e. lethal intergroup violence [1-7].
- Lehmann & Feldman [4] highlighted key role for **kin selection**: self-sacrificing behaviours (e.g. bravery in battle) favoured by selection, even in large groups.
- <u>However</u>: there is scope for **conflicts of interest** over altruistic behaviours in warfare and **sex-specific demography** may impact on the dynamics of war.
- <u>Here</u>: we expand the model in [4], allowing dispersal to evolve and exploring conflicts of interest.
- <u>Life cycle</u>: population divided in groups; i) after birth, subadults may disperse to other groups; ii) each group may engage in warfare with one other group: only males participate in battle; iii) subadults compete for a limited number of breeding spots. Groups that won a war have access to some spots in conquered groups.
- <u>Methods</u>: mathematical modelling; Taylor & Frank's [8] approach to kin selection analysis [9].

Evolution of sex-biased dispersal

- We find that sex-biased dispersal, i.e. sex-specific rates of dispersal, can be driven by:
  - **ecology of warfare**: sex-differences in the spoils of war ($s_f (1 - s_f) \neq s_m (1 - s_m)$) result in differences in dispersal. *E.g.* if females from the winning group do not have access to breeding spots in conquered groups ($s_f = 1$), female-biased dispersal is favoured (see Fig. 1). *Significance*: a <u>novel explanation</u> for atypical female-biased dispersal in mammals that engage in warfare (humans, chimpanzees).
  - **sex-differences in costs**: higher costs of dispersal result in lower rates of dispersal. *E.g.* if females are more readily accepted in foreign groups than are males, this leads to female-biased dispersal.
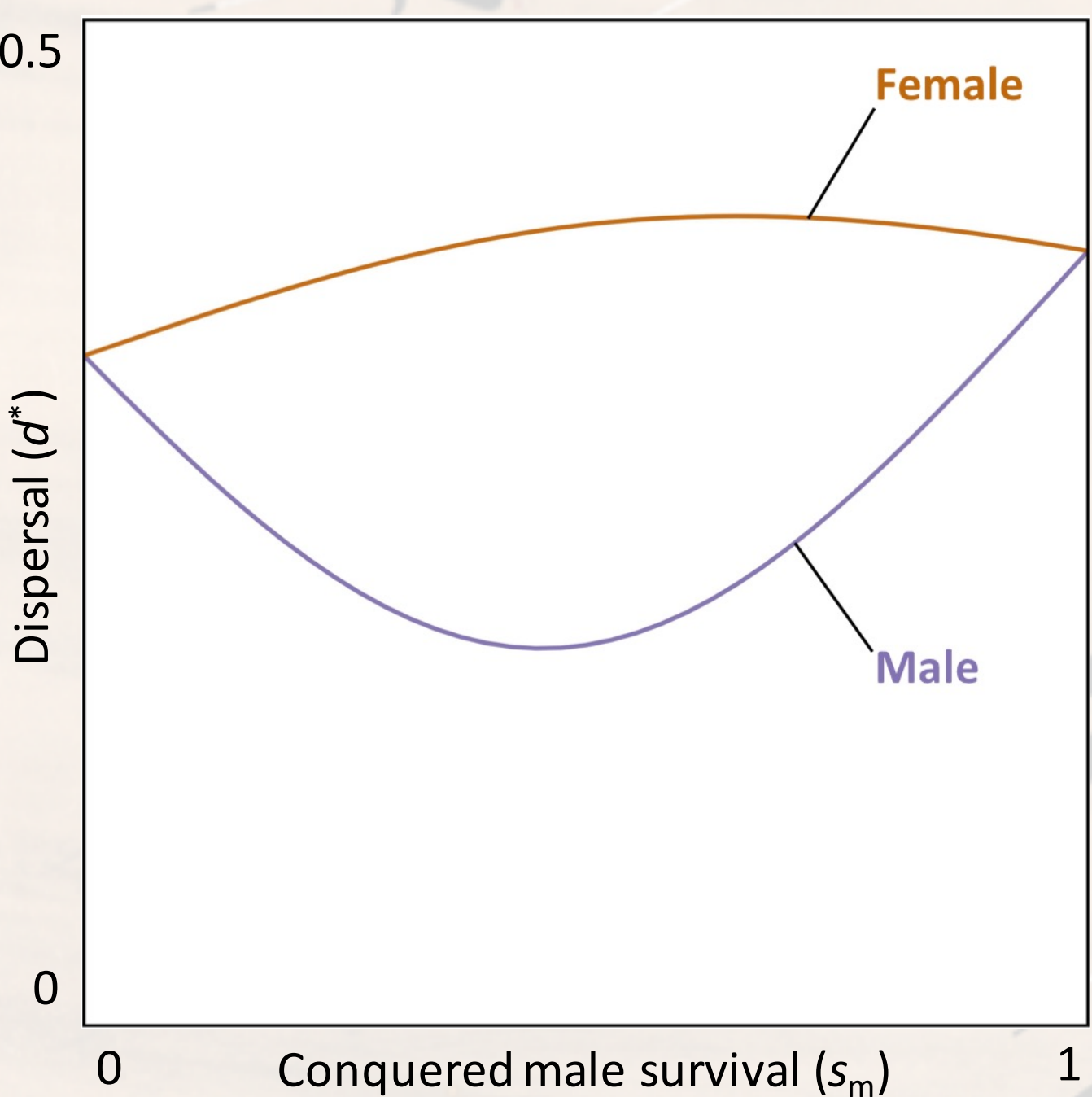
Figure 1 – Evolution of sex-biased dispersal. Convergence-stable levels of female dispersal (d_f^*, orange line) and male dispersal (d_m^*, purple line) as a function of the probability that a conquered male obtains a breeding spot (s_m), when females from the winning group do not get access to breeding spots in the conquered group ($s_f = 1$). Other parameter values are: costs of dispersal $\lambda_f = \lambda_m = 0.05$, number of breeding spots $N_f = N_m = 10$, probability of initiating a war $\bar{a} = 1$, probability of winning a war $\bar{\omega} = 0.5$.

Intrafamily conflict

- We find conflict within the family:
  - **Parent-offspring conflict**: altruism optimum of the warring individual always lower than that of his parents (e.g. bravery, see Fig. 2).
  - **Sexual conflict**: altruism optimum always higher for the parent from the less dispersing sex, because this is more related to offspring's groupmates (e.g. bravery, see Fig. 2).
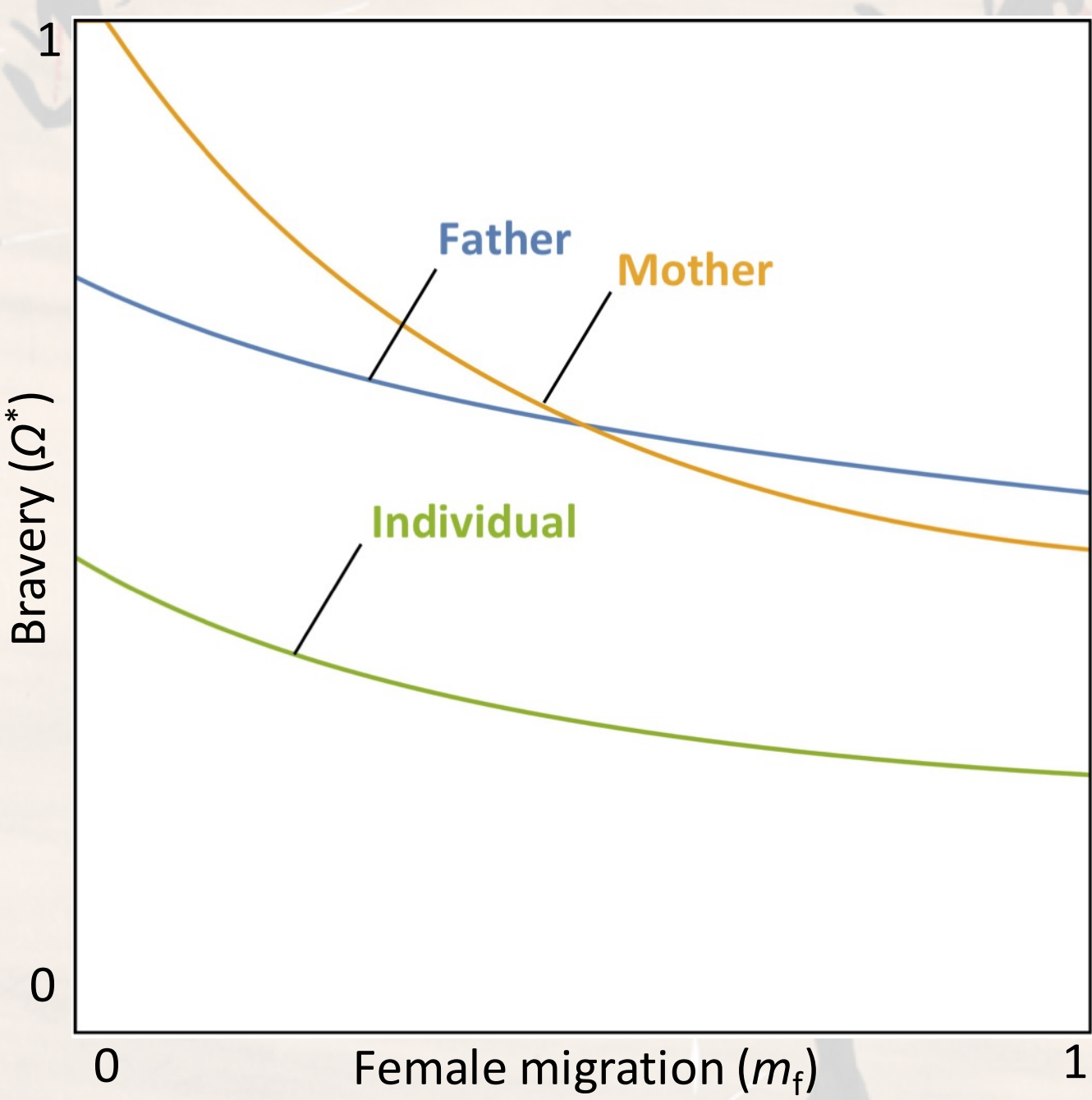
Figure 2 – Intrafamily conflict over bravery. Convergence-stable levels of bravery (Ω^*) as a function of female migration (m_f) when bravery is controlled by the focal male's father (blue line), his mother (orange line), and the focal male himself (green line). Other parameter values are $m_m = 0.5$, $s_f = 1$, $s_m = 0$, $N_f = N_m = 10$. We assume functional forms $\omega(\Omega_{att}, \Omega_{del}) = (1 + \Omega_{att} - \Omega_{del})/2$ and $\tau = 1 - 0.1\, \Omega^{\frac{1}{4}}$ (cost of bravery).

Intragenomic conflict

- We find conflict within the genome of the focal warrior:
  - **Unknown-origin intermediate**: altruism optimum of unknown-origin genes intermediate between that of maternal-origin and paternal-origin genes.
  - **Maternal-origin vs Paternal-origin**: altruism optimum always higher for genes deriving from the less dispersing sex, because they are more related to offspring's groupmates (see Fig. 3).
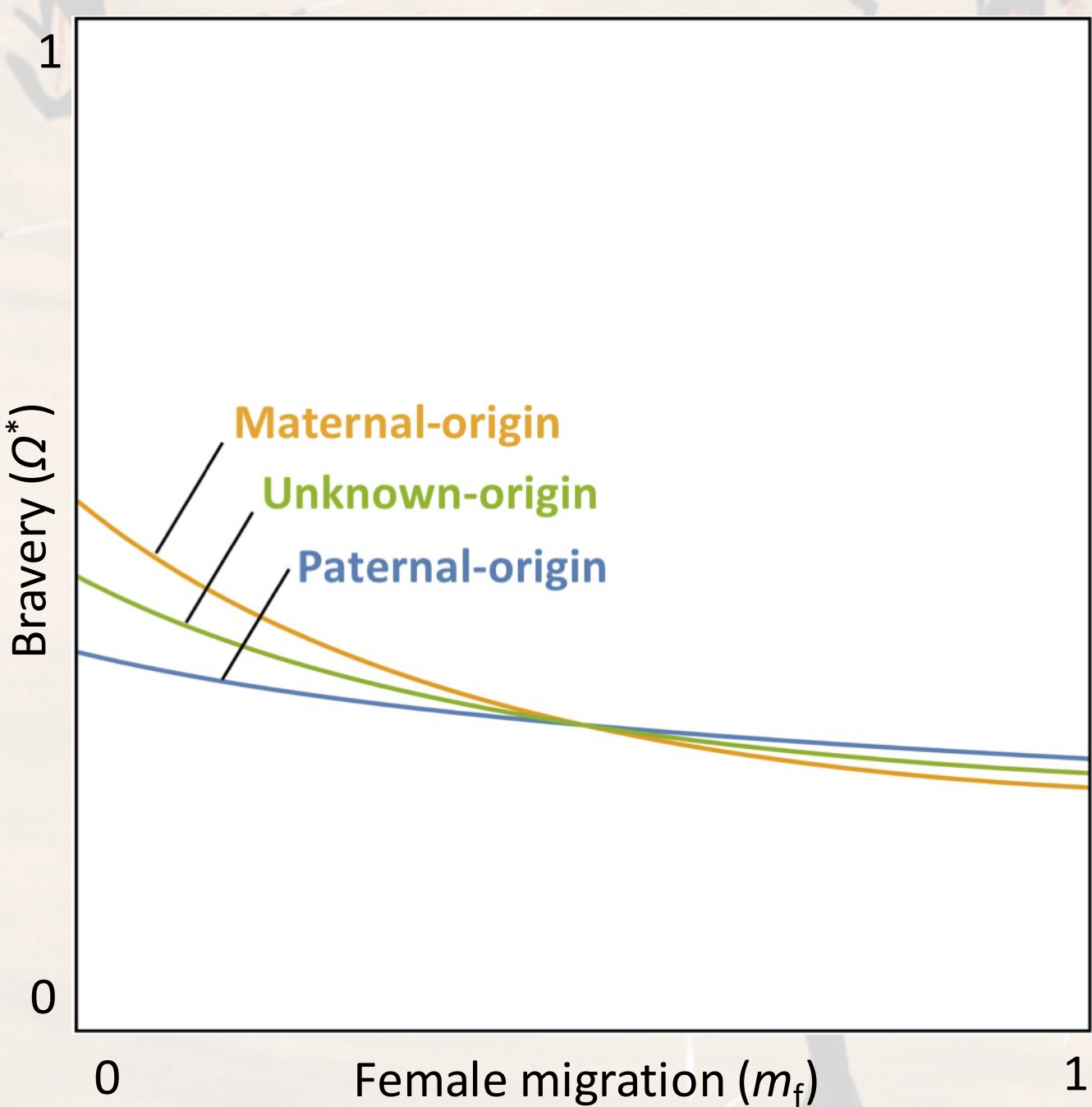
Figure 3 – Intragenomic conflict over bravery. Convergence-stable levels of bravery (Ω^*) as a function of female migration (m_f) when bravery is controlled by the focal individual's paternal-origin genes (blue line), maternal-origin genes (orange line), or unknown-origin genes (green line). Other parameter values are $m_m = 0.5$, $s_f = 1$, $s_m = 0$, $N_f = N_m = 10$. We assume functional forms $\omega(\Omega_{att}, \Omega_{del}) = (1 + \Omega_{att} - \Omega_{del})/2$ and $\tau = 1 - 0.1\, \Omega^{\frac{1}{4}}$ (cost of bravery).

Genomic imprinting and associated pathologies

- Conflict can be resolved by the evolution of genomic imprinting, i.e. parent-of-origin-specific expression of genes [10-12]. Can predict patterns of expression [10].
- Under female-biased migration, for a promoter locus: gene with the lower optimum is silenced ($\times$), the other **expressed** ($\rightarrow$) at its optimum (see Fig. 4)
- Being imprinted, these loci are functionally haploid and thus exposed to **deleterious mutations**. These may lead to abnormal phenotypes and pathological conditions. In the case of bravery: 'reckless' (abnormally high bravery) or 'cowardly' (abnormally low bravery). We make expression predictions in Fig. 4.

Figure 4 – Genomic imprinting and associated pathologies. Predicted patterns of parent-of-origin-specific gene expression and concomitant phenotypes for loci that are either promoters or inhibitors of bravery, under normal conditions and also as a result of three different mutational or epimutational perturbations: gene deletion, imprinting disruption, uniparental disomy. Genes are either maternal-origin (orange) or paternal-origin (blue), and are either silenced (crosses) or expressed (arrows). Human figures from the George Stow collection at Iziko South African Museum, derived from *The Digital Bleek and Lloyd* (lloydbleekcollection.cs.uct.ac.za) with permission.

Conclusions

- **Ecology of war** leads to sex-biased dispersal: novel explanation for female-biased dispersal in ancestral humans, hunter-gatherers, African apes.
- Intense **intrafamily conflict**: parent-offspring and parent-parent. Who controls warfare matters.
- Intense **intragenomic conflict** can be resolved by the evolution of **genomic imprinting**. Associated mutations may generate **pathological phenotypes**: might help explaining societally-damaging intergroup violence.

References: [1] Kelly RC, 2005, *PNAS*, 102, 15294-8; [2] Gat A, 2006, *War in human civilisation*; [3] Choi JK, Bowles S, 2007, *Science*, 318, 636-40; [4] Lehmann L, Feldman MW, 2008, *ProcRSocB*, 275, 2877-85; [5] Bowles S, 2009, *Science*, 324, 293-8; [6] Wrangham RW, Glowacki L, 2012, *HumNat*, 23, 5-29; [7] Johnson DDP, Toft MD, 2014, *IntSecurity*, 38, 7-38; [8] Taylor PD, Frank SA, 1996, *JTheorBiol*, 180, 27-37; [9] Hamilton WD, 1964, *JTheorBiol*, 7, 1-52; [10] Haig D, 1996, *JEvolBiol*, 9, 357-80; [11] Haig D, 2002, *Genomic imprinting and kinship*; [12] Haig D, Úbeda F, 2003, *Genetica*, 117, 103-10.

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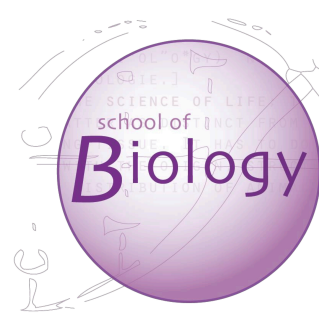
Sex differences in altruism and the demography of human warfare

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Introduction

- Recent years have seen an increasing interest in understanding the possible links between warfare and within-group altruism [1].
- Parochial Altruism (PA): intersection of 'outgroup hate' & 'ingroup love' – there can be selection for altruism in the context of war [2].
- At the same time: studies suggesting that sex is an important modulator of social behaviours in the context of warfare [3,4].
- However: sex differences in altruism in the context of warfare have been neglected by PA. Might be driven by demography?
- Here: we asses whether sex differences in demography (dispersal & movement of individuals between groups as a result of war) can lead to sex differences in altruism in populations experiencing warfare.

Model

- We adapt and expand a kin selection model of warfare by [3-5].

- Life cycle: population divided in groups with Wright-Fisher process i) after birth, young adults disperse to random groups with sex-specific probabilities m_m & m_f; ii) social interaction: males and females may act altruistically towards groupmates; iii) each group may engage in warfare with one other group: only males participate in battle; iv) subadults compete for a limited number of breeding spots.

- After war: Individuals from victorious groups have access to *a fraction* of breeding spots in defeated groups. Admixture: extent to which adults in a group, in next generation, are a mix of winners and losers. May be different for men and women: M_m & M_f.

- Definition of altruism: any behaviour that increases the receiver's competitiveness for breeding opportunities while decreasing that of the altruist (e.g. helping with foraging/farm work; sharing resources).

- Analysis: neighbour-modulated fitness approach to kin-selection analysis; Taylor & Frank's maximisation method [6].

Altruism

- **Q1**: which sex helps more? & **Q2**: which sex is helped more?
- Consider: Altruism male-to-male **mm**   Altruism male-to female **mf**
  Altruism female-to-male **fm**   Altruism female-to-female **ff**

- For example, male-to-female altruism is favoured to increase if:

$$-c + \alpha_m c\, r_{mm} + b\, r_{mf} - \alpha_f b\, r_{mf} > 0$$

- Rearranging: $c/b < A_{mf}$ where:

$$A_{mf} = \frac{r_{mf} - \alpha_f\, r_{mf}}{1 - \alpha_m\, r_{mm}}$$

- is "potential for altruism" – Highlights dependence on demography.
- c is marginal cost to altruist; b is marginal benefit to recipient.
- r_{mm} is relatedness between males; r_{mf} is relatedness male-female.

- $\alpha_i = 1 - 2a\omega M_i$ is the extent to which sex-i individuals compete for reproduction with same-sex groupmates (i.e. 'locally') as opposed to competing with individuals in other groups (i.e. 'globally').
  ** Differences between male and female α depend on admixture **

Results: dispersal & admixture

- Result 1 Dispersal – The more philopatric sex are more altruistic because they have higher relatedness to the group. Individuals of the more philopatric sex also receive more altruism, because both sexes are more related to them than to the more dispersing sex.

- Result 2 Admixture – The *lower-admixture sex* is more altruistic because, competing more locally, has more to gain by releasing kin competition through altruism. It is instead individuals of the *higher-admixture sex* that receive more altruism. As they compete more globally, by helping them, an altruist has the chance to increase a groupmate's competitiveness without increasing kin competition as much as for the other sex.
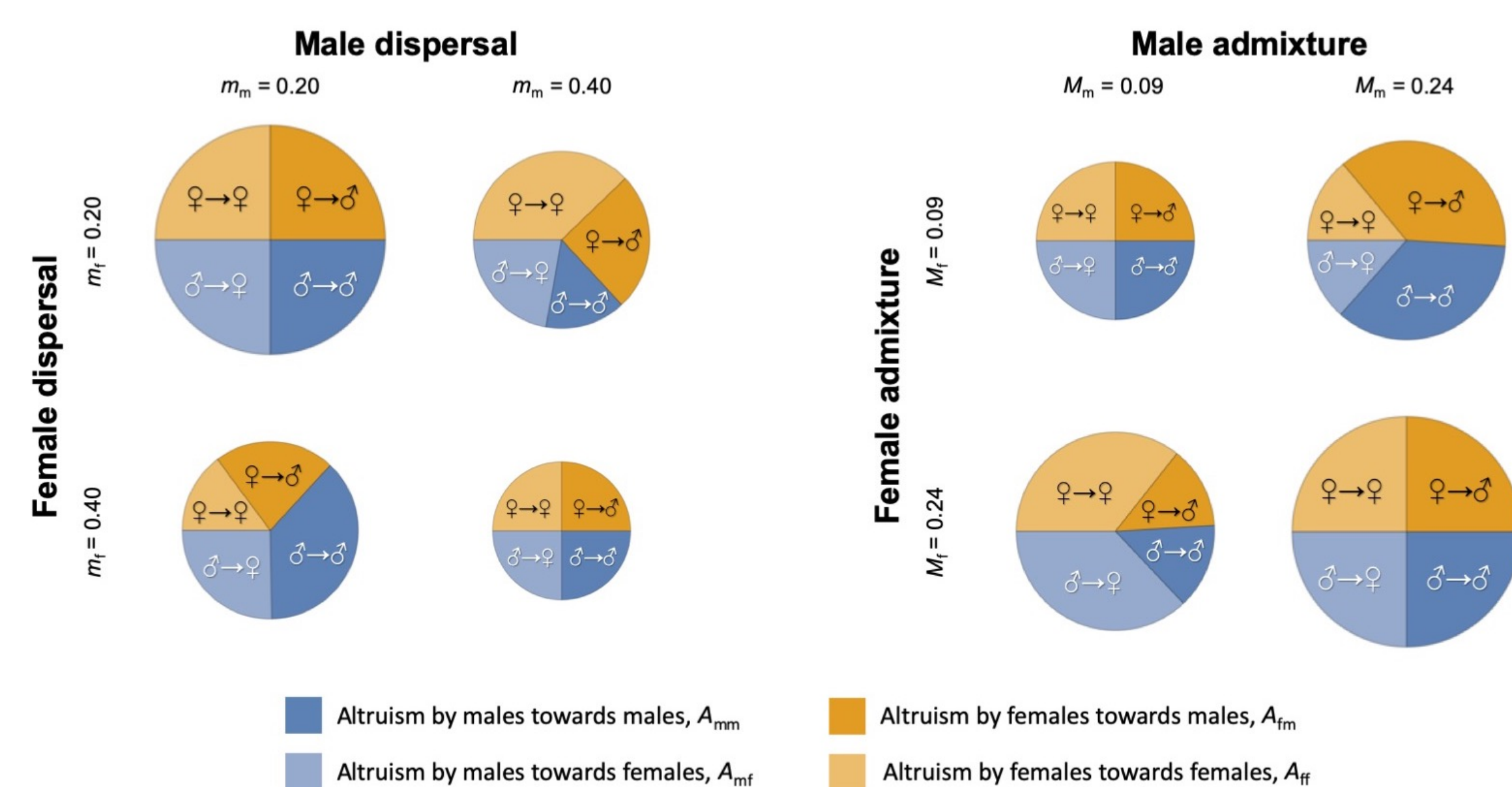

Demography influences patterns of altruism in the context of war

- The two demographic parameters can reinforce each other or act in opposing directions

We identify four patterns of sex-specific altruism – four systems:

- ♠ *Boys' Club systems* – men more altruistic and receive more altruism
- ♦ *Girls' Club systems* – women more altruistic and receive more altruism
- ♥ *Men-help-Women-helped systems* – men are more altruistic, women receive more altruism
- ♣ *Women-help-Men-helped systems* – women are more altruistic, men receive more altruism
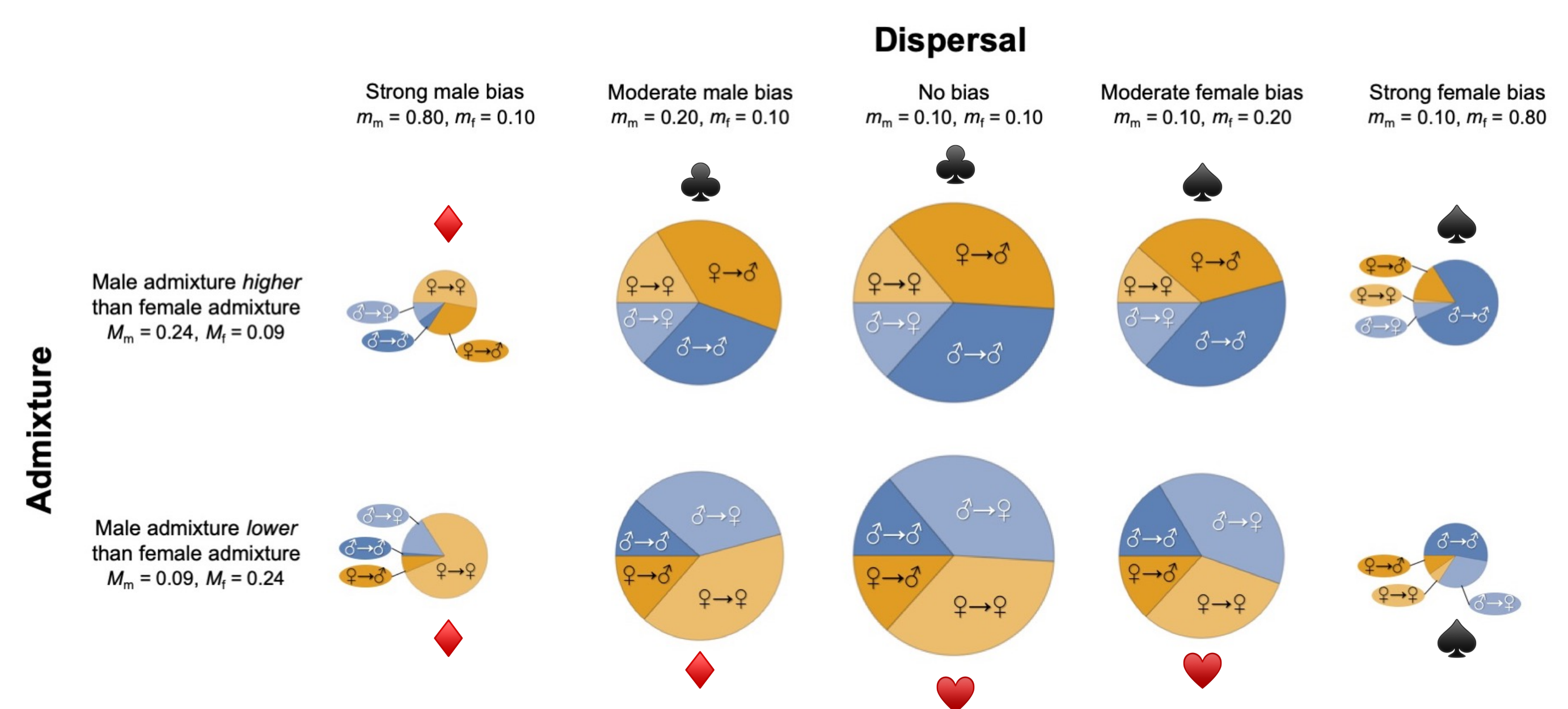
Conclusions

- Sex is a fundamental modulator of altruism in populations experiencing intergroup warfare.
- The more philopatric sex is favoured both to be more altruistic and to receive more altruism.
- The sex that competes more locally (lower admixture) is favoured to be more altruistic, the sex that competes more globally (higher admixture) is favoured to receive more altruism.
- A past of warfare and intergroup conflict, together with sex-biased demography, can help explain observed patterns of cooperation and altruism in small-scale societies.

References: [1] Rusch H, 2014, *ProcB*, 281, 20141539; [2] Choi JK, Bowles S, 2007, *Science*, 318, 636-40; [3] Micheletti AJC, Ruxton GD, Gardner A, 2017, *ProcB*, 284, 20162699; [4] Micheletti AJC, Ruxton GD, Gardner A, 2018, *ProcB*, 285, 20180975; [5] Lehmann L, Feldman MW, 2008, *ProcRSocB*, 275, 2877-85; [6] Taylor PD, Frank SA, 1996, *JTB*, 180, 27-37;
Other: painting above from the George Stow collection at Iziko South African Museum, derived from *The Digital Bleek and Lloyd*.