# Evolutionary consequences of knitting with one needle: The point of genomic imprinting

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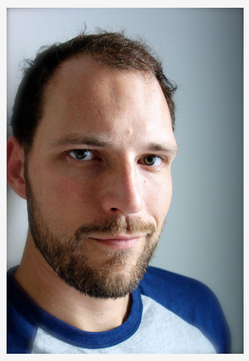
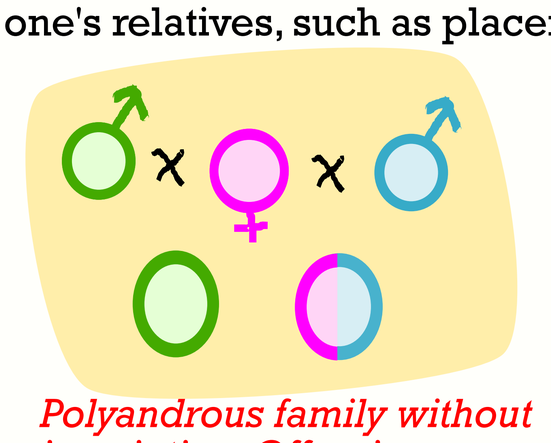


Genomic imprinting is a somewhat rare genetic phenomenon in which an allele "remembers" which parent it came from, and shows differential expression. Typically, one parent's allele is silent and the locus expresses only one allele. This leaves the locus fully exposed to deleterious recessives, as well as a host of other costs.

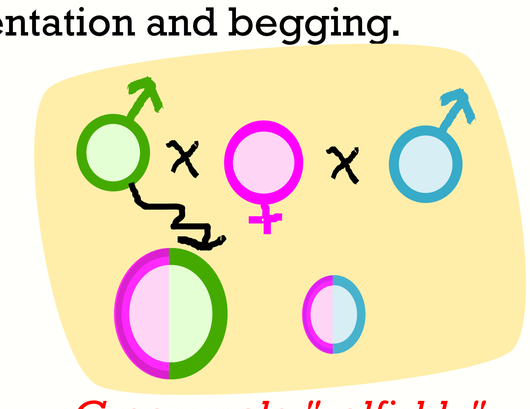
## Given its substantial costs, why did genomic imprinting evolve?

### The kinship theory

Maternally- and paternally-inherited alleles are differentially related to the focal individual's kin. For example, the two sets of alleles have different chances to be present in the individual's half-siblings. This creates intra-genomic conflict over traits affecting the fitness of one's relatives, such as placentation and begging.



*Polyandrous family without imprinting. Offspring are provisioned equally*

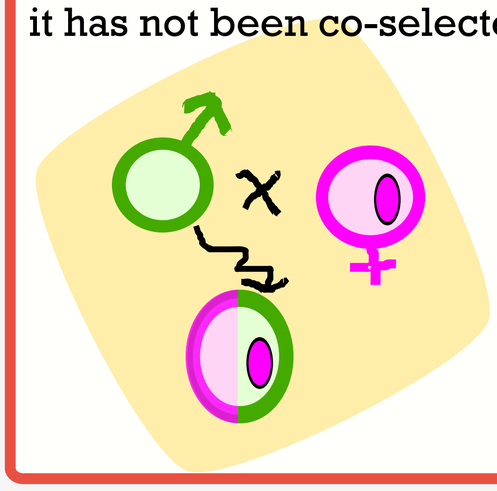


*Green male "selfishly" imprints a growth inhibiting allele*

Haig 2000

### The co-adaptation theory

Imprinting might improve levels of co-adaptation when loci interact. There are several versions of this theory; one example involves cyto-nuclear epistasis. Imagine that fitness depends on having complementary alleles at a pair of nuclear and mitochondrial loci. Selection might favour imprinting of the paternal nuclear allele, because it has not been co-selected with the mitochondrial allele.

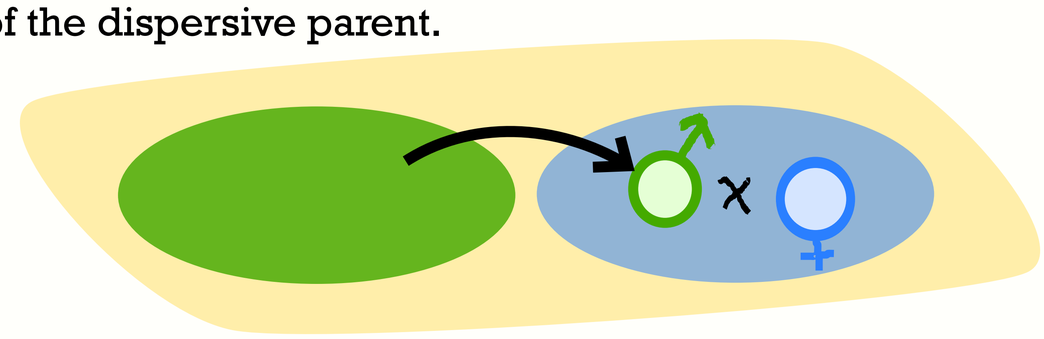


*Male imprints his allele at a nuclear locus that interacts epistatically with the maternally-inherited cytoplasmic gene. Therefore, only the co-adapted maternal copy is active.*

Wolf 2009, 2013; Wolf and Hager 2006, 2009

### The parental resemblance theory

Sometimes, one parent is consistently better adapted than the other. For example, if there is sex-biased dispersal and selection favours different traits in different areas, the more sedentary parent will tend to be more locally adapted. Therefore, it might pay offspring to imprint the allele of the dispersive parent.

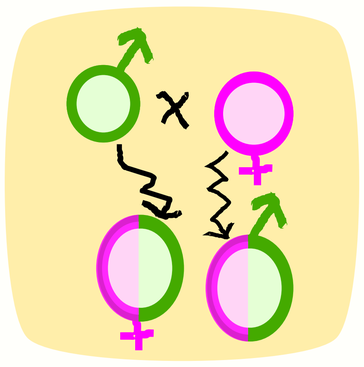


*In this species, males are more migratory. The green male is maladapted to his mate's environment, so he might benefit from imprinting alleles at loci affecting local adaptation.*

Spencer and Clark 2006

### The gender load theory

"Gender load" occurs when males and females are selected to produce different trait values, but are constrained from doing so by inter-sex genetic correlations. Imprinting might allow individuals to reduce the gender load. For example, males might imprint alleles from their mother, and females imprint alleles from their father. Each sex could thereby utilise an allele that survived selection in its same-sex parent.



*Individuals might imprint alleles inherited from their opposite sex parent, since the same-sex parent is expected to have better adapted alleles.*

Day and Bonduriansky 2004

### How can we make sense of genomic imprinting?

***Which benefit explains the evolution of imprinting?***

Each of the theories presented here are apparently plausible, and have received varying degrees of empirical support. However, the hypotheses are not mutually exclusive: multiple mechanisms might favour imprinting at different loci, or at any given locus.

There are many other theories, but some can be ruled out; e.g. imprinting was proposed to increase evolvability by increasing levels of genetic variation, but simple models show it actually reduces variation when most mutations are recessive.

***What should we do next?***

Empirical tests of the theories of imprinting have been quite indirect. There is a need for experiments, e.g. manipulating the imprinting status of a locus and testing the fitness consequences.

There is also room for more theory. For example, the adaptation-based hypotheses require that there is genetic variation at the imprinted loci, otherwise imprinting will do little to improve adaptation. Whether enough variation is expected to exist is unknown.

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