



Can the Fisher-Lande Process Account for Birds-of-Paradise and Other Sexual Radiations?

$$\begin{pmatrix} \Delta \bar{z} \\ \Delta \bar{y} \end{pmatrix} = \begin{pmatrix} G & B \\ B & H \end{pmatrix} \begin{pmatrix} \beta_z \\ \beta_y \end{pmatrix} \quad \longleftrightarrow$$



Stevan J. Arnold & Lynne D. Houck

Department of Integrative Biology

Oregon State University

Argument

- Models of the FLP have been successful, but
- Their predictions are seldom (never?) tested.
- The Phenotypic Tango, a more general version of the model, offers some improvements.
- Its predictions can be evaluated with simulations, but
- Can the Phenotypic Tango account for actual sexual radiations (e.g., the bird-of-paradise radiation)?
- What about popular generic models (BM & OU)? Can they account for the b-o-p radiation?
- Conclusions
- Some directions for the future



Fisher's Insight



Ronald A. Fisher (1890-1962)

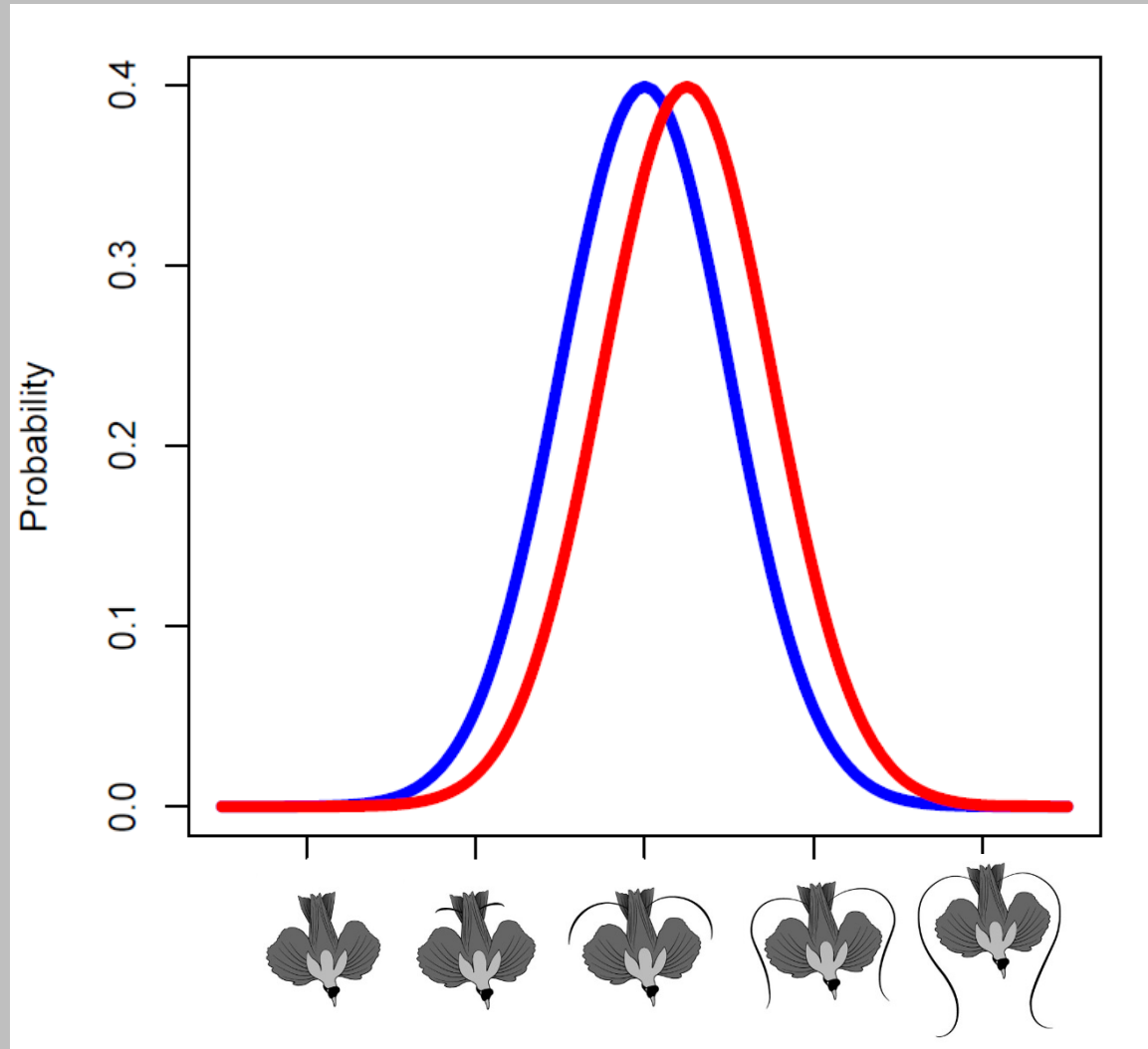
“The two characteristics affected by such a process, namely plumage development in the male, and sexual preference for such development in the female, must thus advance together ... with ever-increasing speed.”

Fisher 1915, 1930

*Lande's model: coevolving within-population distributions of **ornaments** and **preferences***



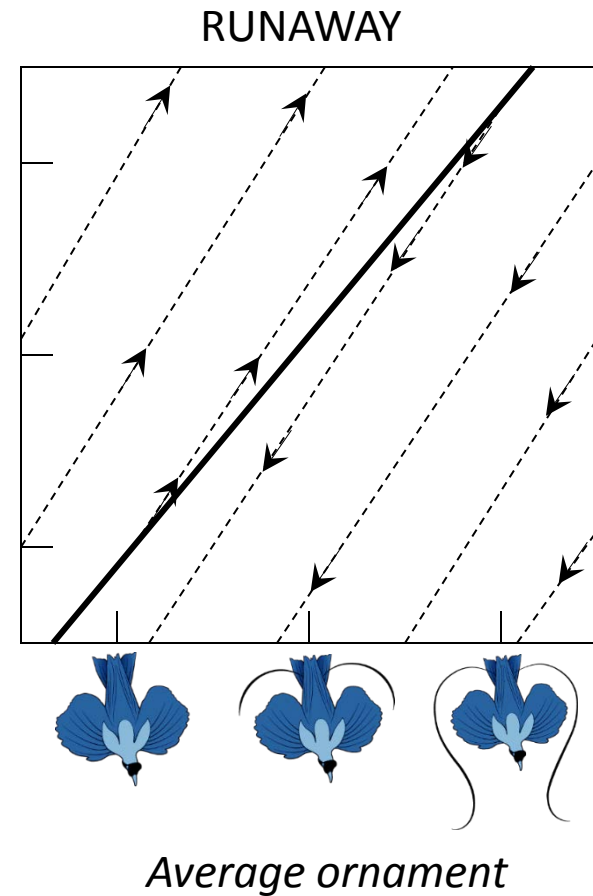
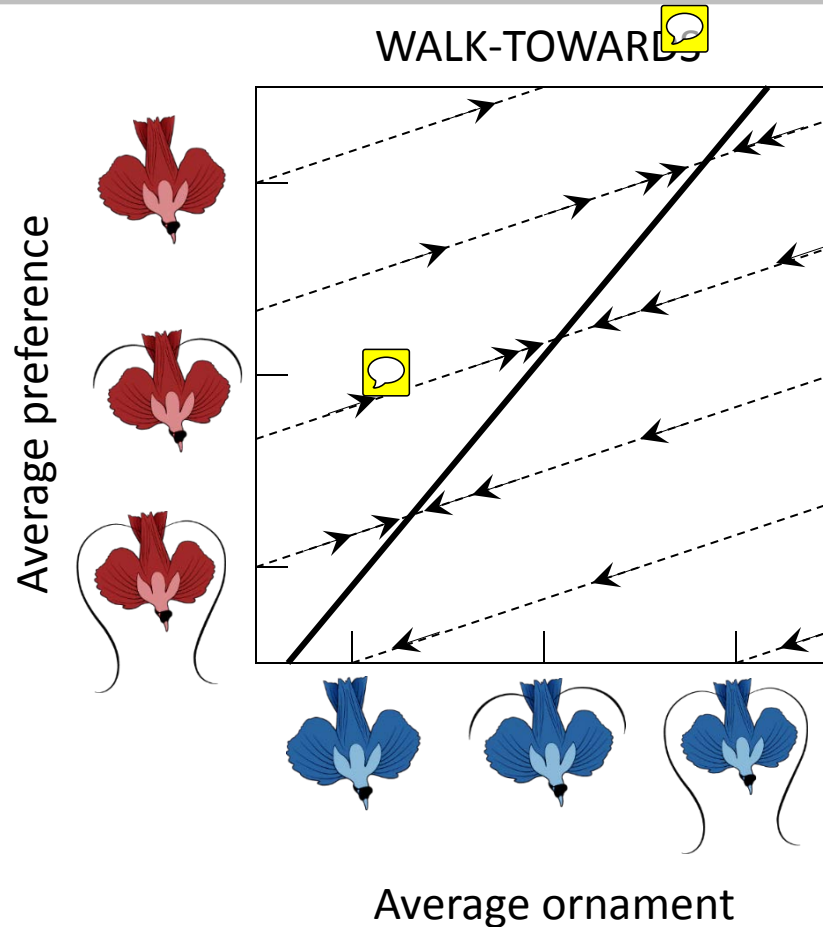
Russell Lande



Ingredients of the Fisher-Lande Process

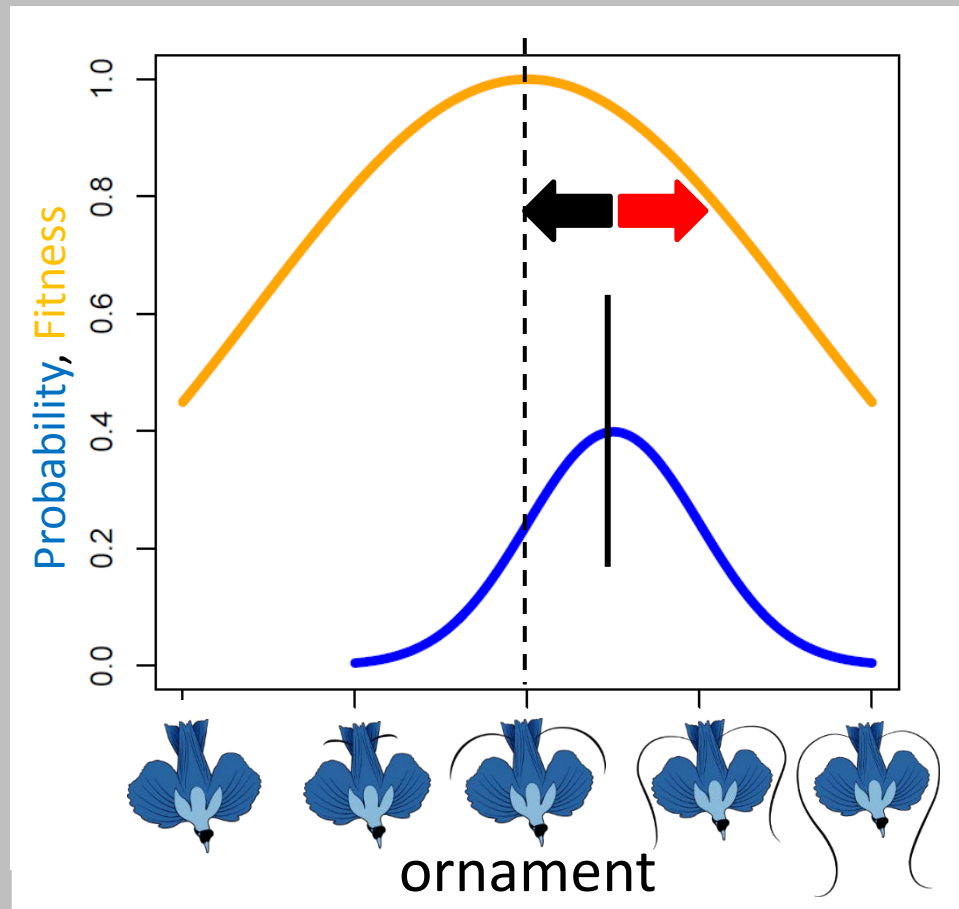
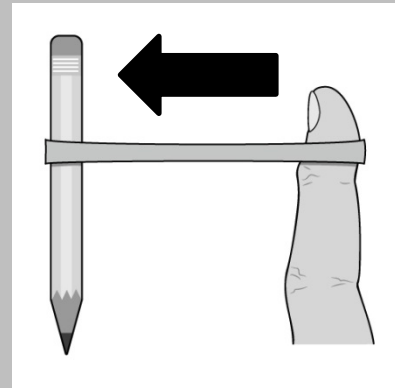
- A male **ornament** affects male survival and – via female preference - mating success,
- Female mating **preference** is based on the ornament but does not affect the survival or fecundity of the female.
- Both traits are heritable and – because of assortative mating and sexual selection on males – genetically correlated.

Walk-towards and Runaway Outcomes





***Stabilizing natural selection
towards an intermediate
ornament optimum
balanced by
opposing
sexual
selection***

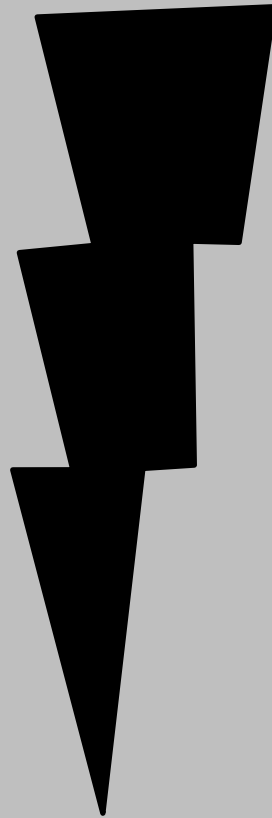




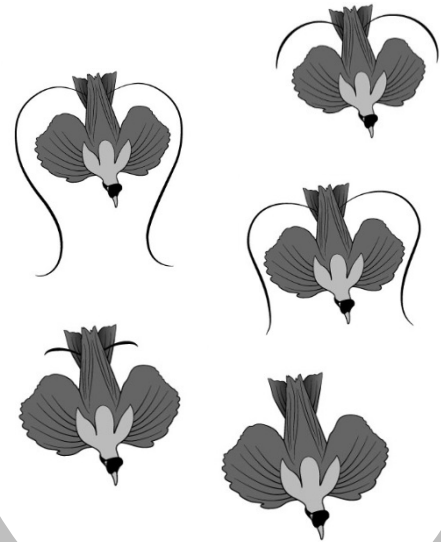
Problem: failure to connect the models with real sexual radiations

models

$$\begin{pmatrix} \Delta \bar{z} \\ \Delta \bar{y} \end{pmatrix} = \begin{pmatrix} G & B \\ B & H \end{pmatrix} \begin{pmatrix} \beta_z \\ \beta_y \end{pmatrix}$$



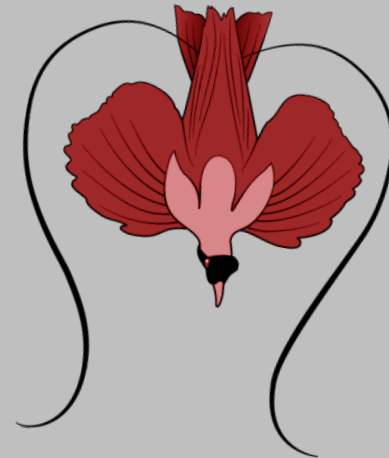
nature



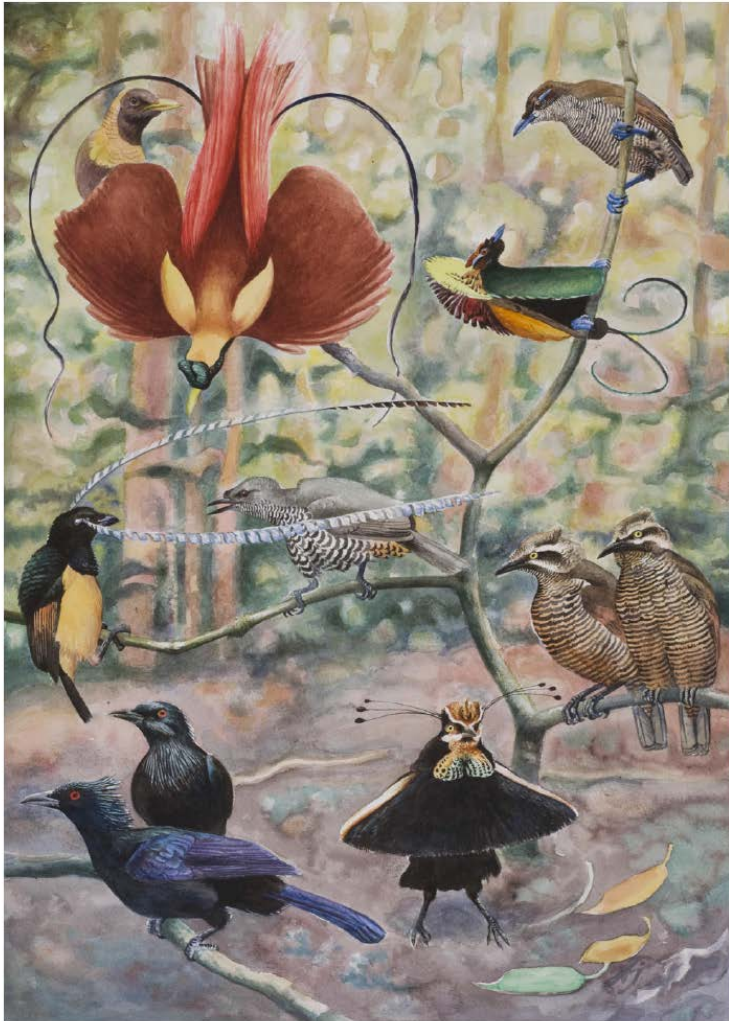


Solution: Birds-of-Paradise, an Iconic Sexual Radiation

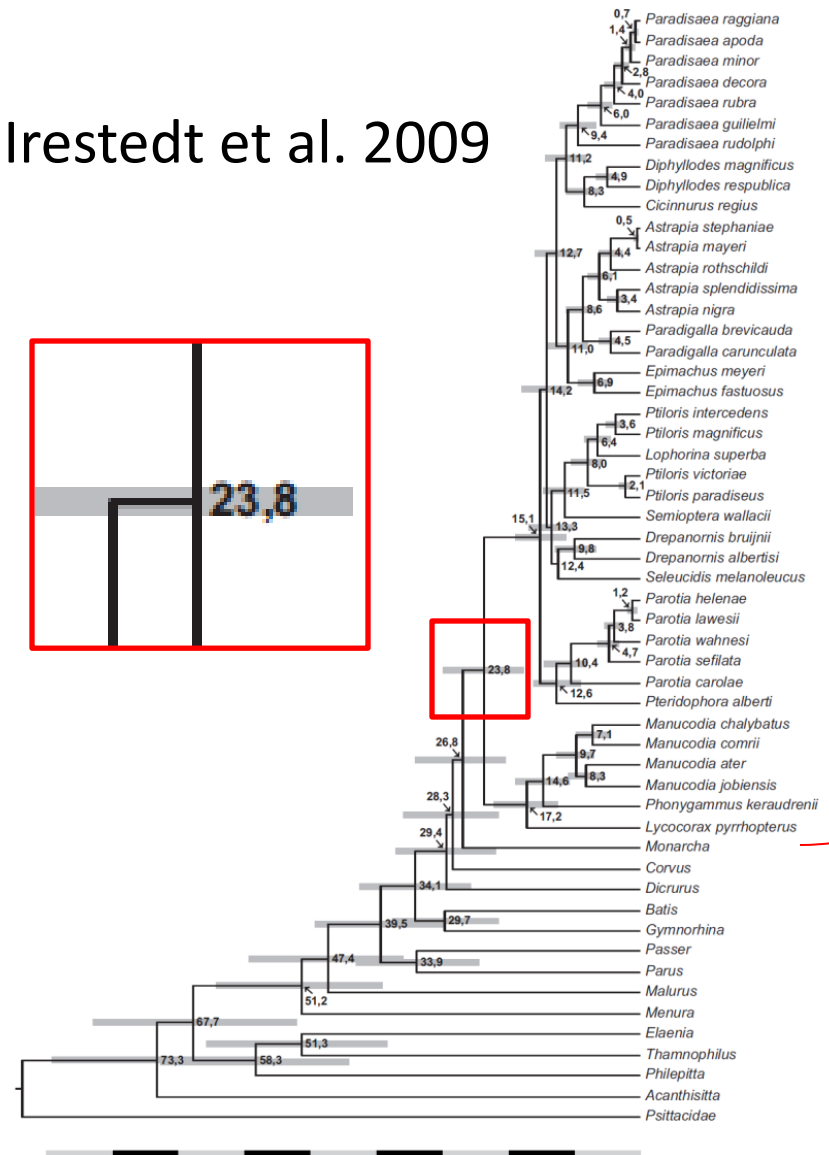
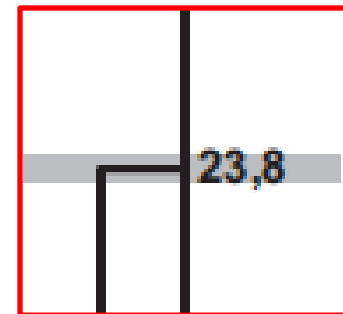
- Time-calibrated phylogeny
- Male display and female choice
- Morphological components of male display
- Data on male morphology



Diversification over 23 million years



Irestedt et al. 2009



Special features of plumage presented during male displays

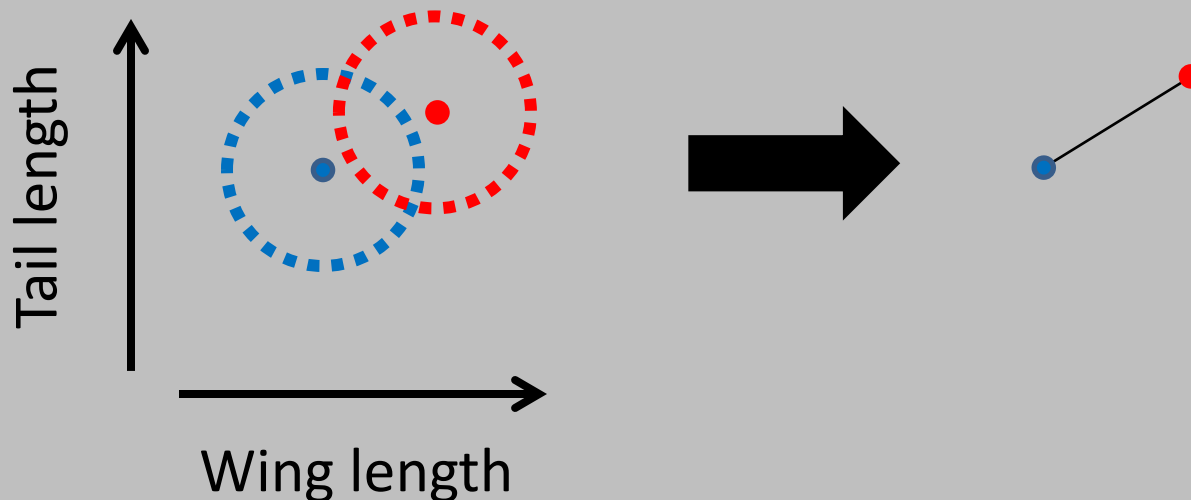


<https://www.facebook.com/Birds.Lovers.1/videos/1003571246388699/>

Phenotypic tango: a more general model of the FLP

- Two male display traits (**ornaments**)
- Two female **preference** traits
- Selection on female preference
- Finite population size

Graphical Conventions



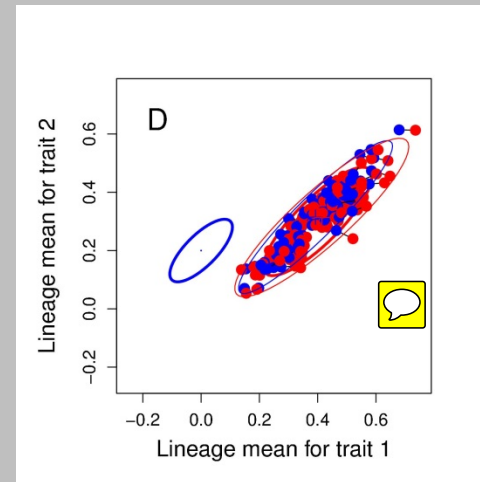
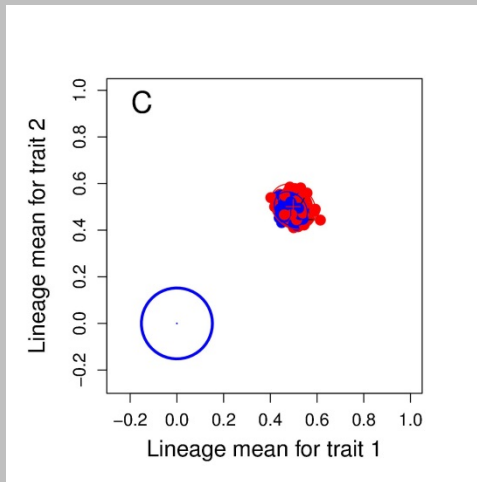
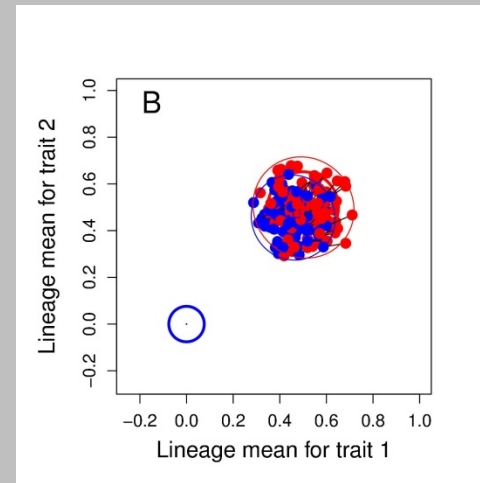
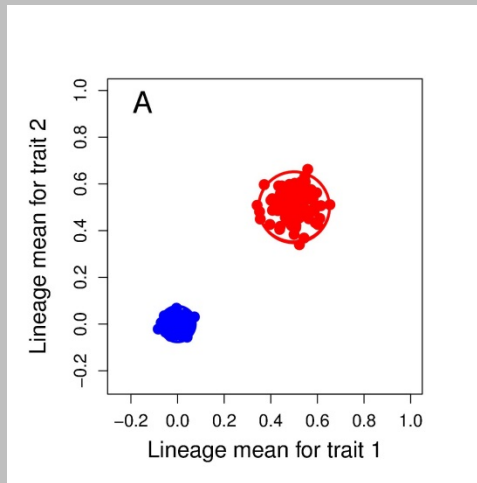


Phenotypic tango: a more general model of the FLP

- GOOD NEWS! - Model more general than past versions
- BAD NEWS! – No analytical solution for model
- MORE GOOD NEWS! – Can determine the model's behavior with simulations



Phenotypic tango: evaluating the model's behavior with simulations





Phenotypic tango: evaluating the model's behavior with simulations

For animations, see

<http://phenotypicevolution.com/?p=221>

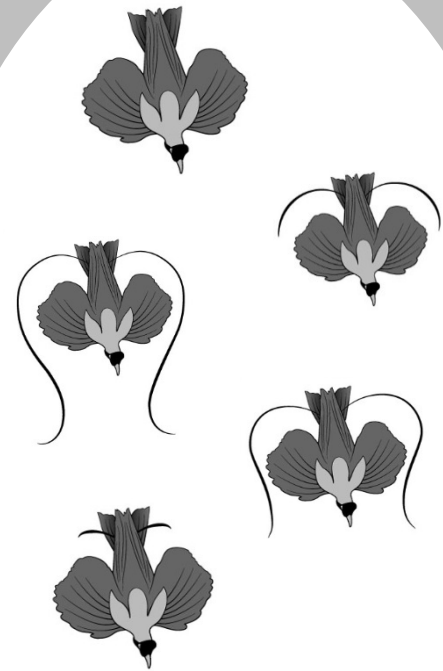
These animations will not run in Chrome



Accounting for the Bird-of-Paradise radiation with the *Phenotypic Tango* model

$$\begin{pmatrix} \Delta \bar{z} \\ \Delta \bar{y} \end{pmatrix} = \begin{pmatrix} G & B \\ B & H \end{pmatrix} \begin{pmatrix} \beta_z \\ \beta_y \end{pmatrix}$$

data





Phenotypic differentiation in the genus *Paradisaea* over 9 million years



rudolphi



guilielmi



rubra



decora



minor

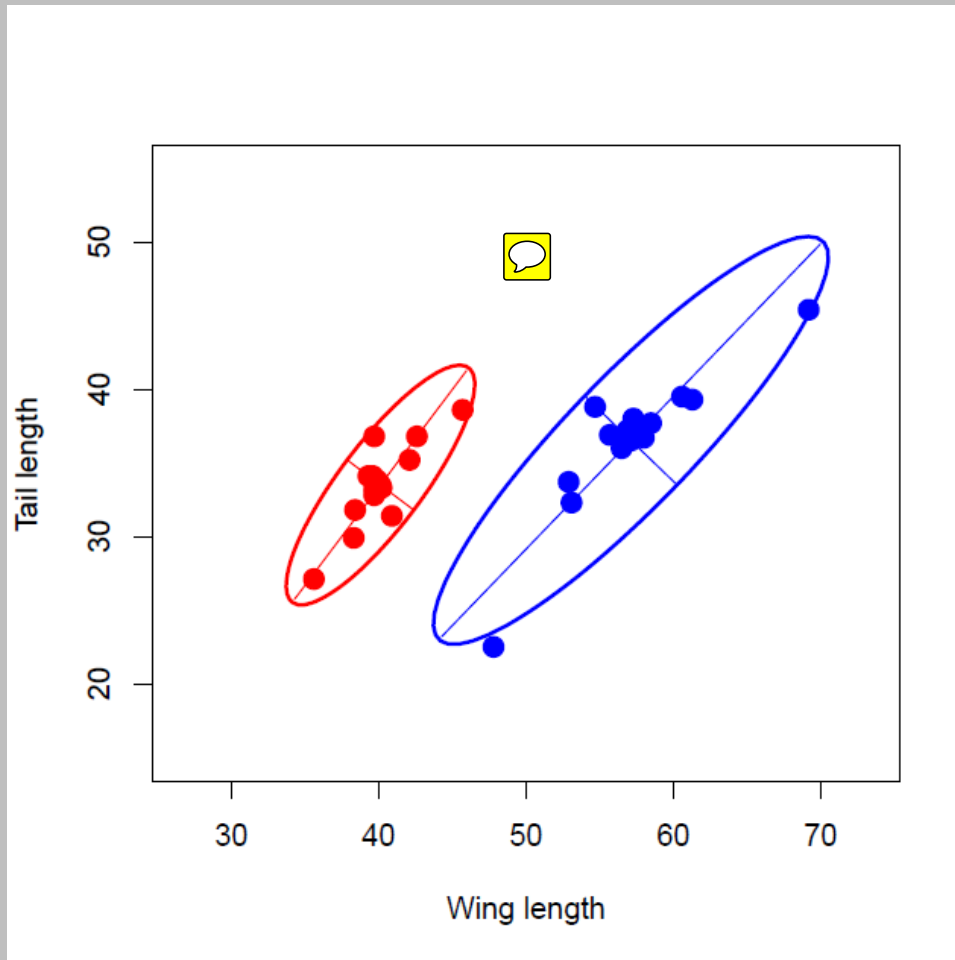


apoda



raggiana

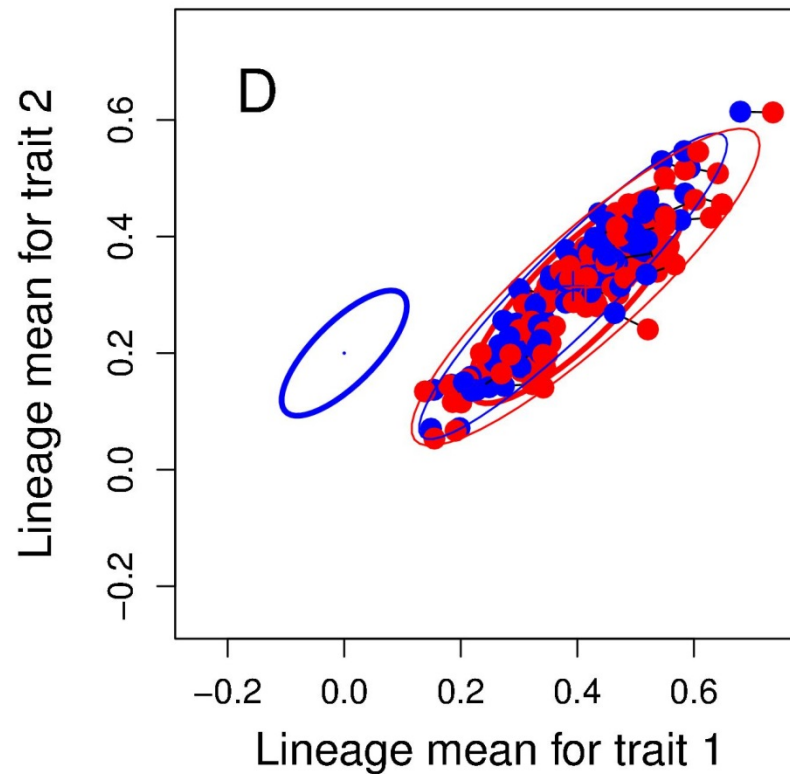
How much evolution? ± 12 phenotypic standard deviations in 188,000 generations



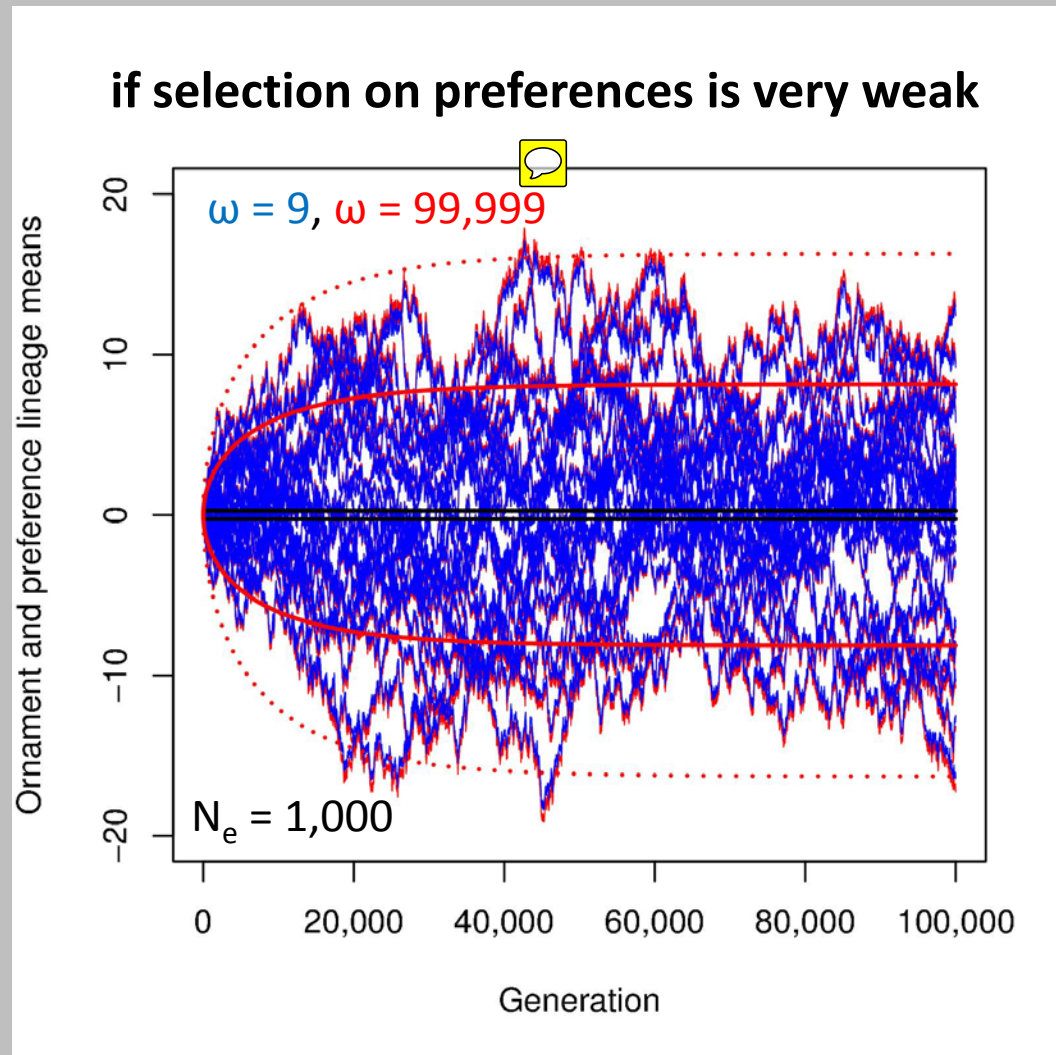
Mary LeCroy



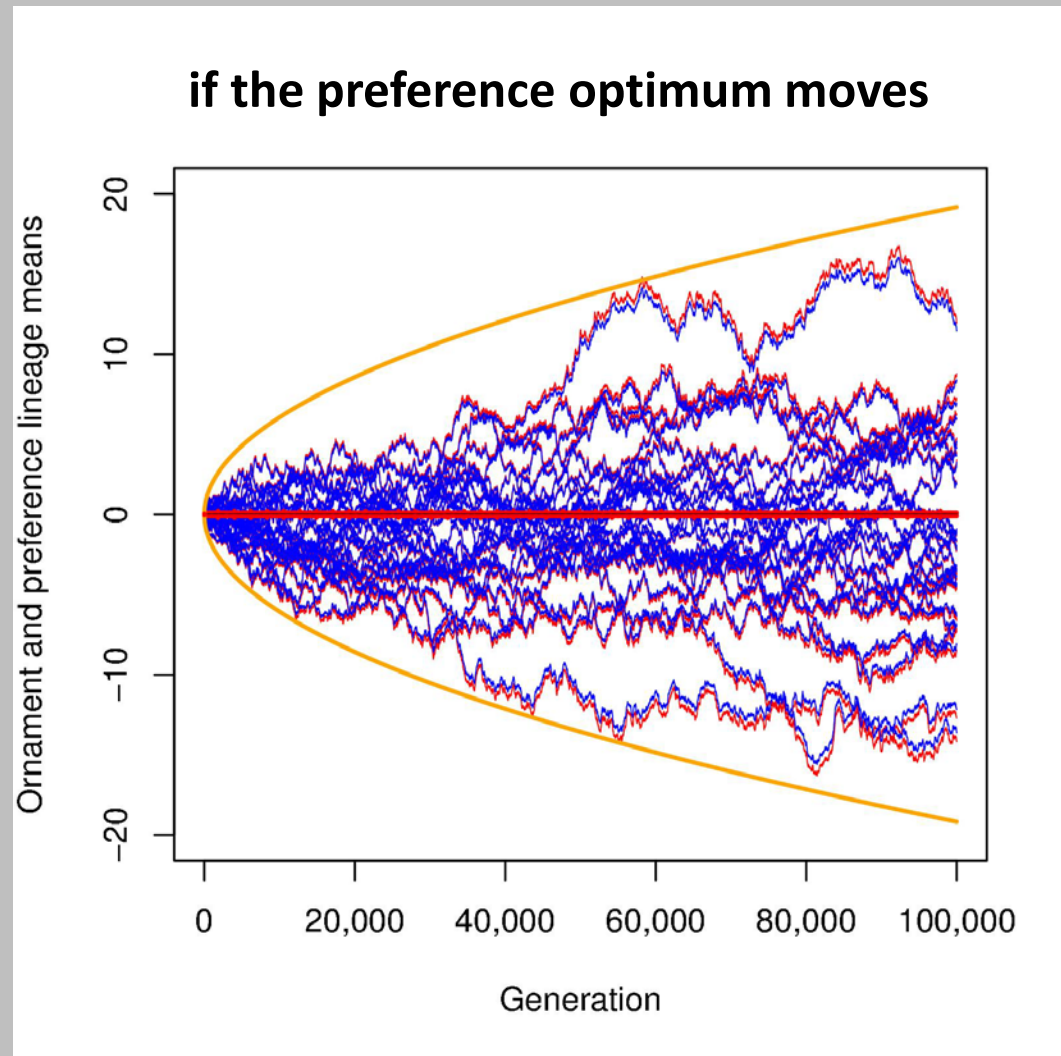
*The **Phenotypic Tango** can account for bivariate patterns in the data*




The *Phenotypic Tango* can account for the observed amount of diversification



The *Phenotypic Tango* can account for the observed amount of diversification




*Conclusions using the **Phenotypic Tango** model*

- Evolving preferences control the evolution of ornaments
- Can account for diversification **patterns** in single and multiple ornaments
- To account for the **extent** of ornament diversification on right timescale, we need to invoke:
 - Very weak stabilizing selection on preferences and relatively small effective population sizes
 - Or natural selection optima must move at a modest rate 



*Accounting for the Bird of Paradise radiation with **generic models**: Brownian motion & Ornstein-Uhlenbeck*

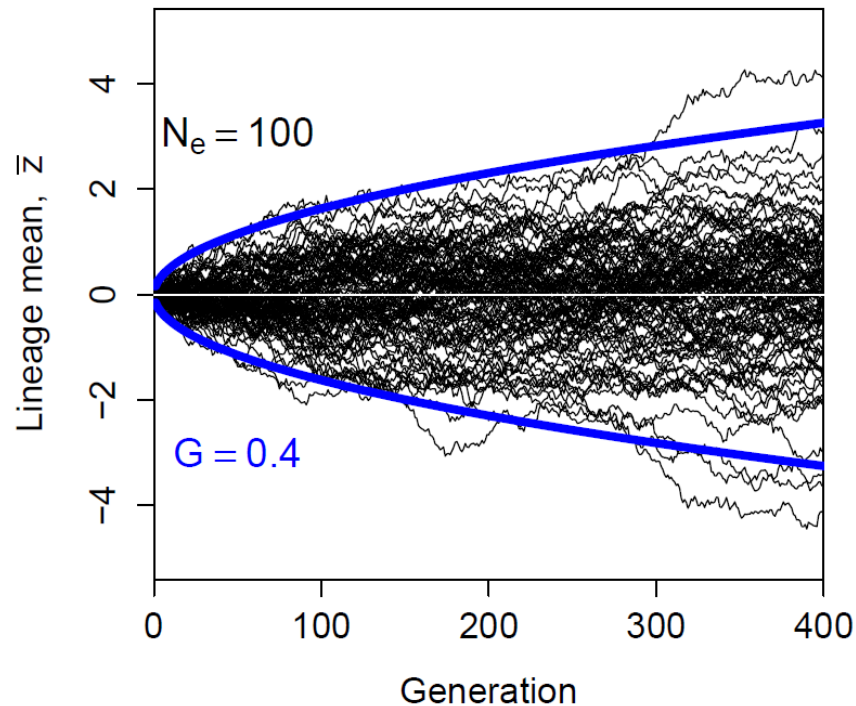
- GOOD NEWS! – Analytical solutions available.
- BAD NEWS! – The parameters we estimate confound inheritance, selection, and pop. size. 
- GOOD NEWS! – We can account for phylogeny.
- GOOD NEWS! – We can use likelihood to compare alternative models

*Accounting for the Bird-of-Paradise radiation with **generic models***

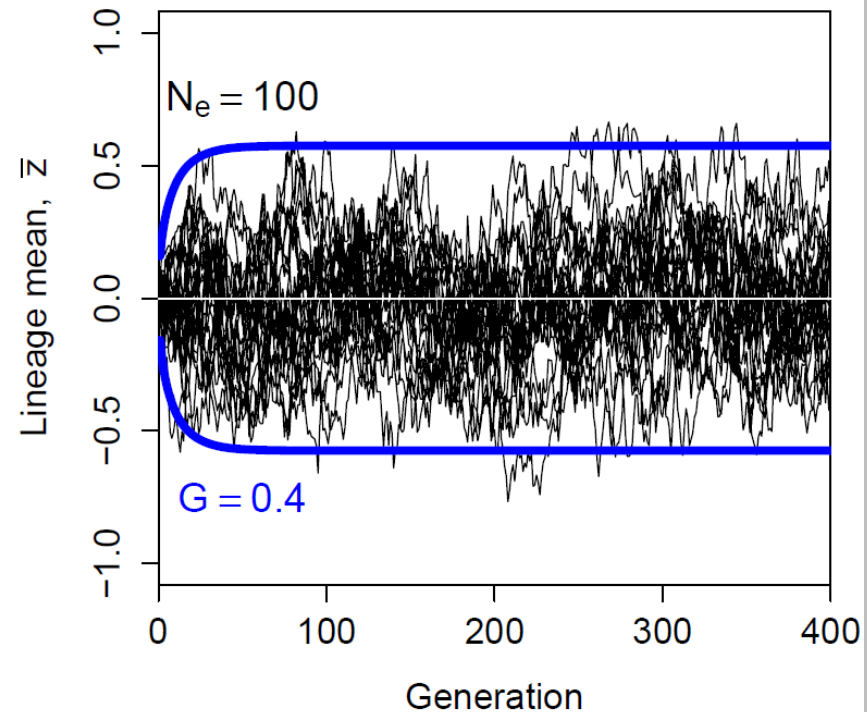
- The contrast between Brownian Motion (BM) and Ornstein-Uhlenbeck (OU) models
- Testing model predictions on the Bird-of-Paradise tree
- Do we need more than one selection regime (poor man's version of moving optimum) to account for the data?
- Can we use this framework to estimate FLP parameters?

Contrasting model predictions

BM -> ever-expanding evolution

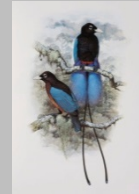
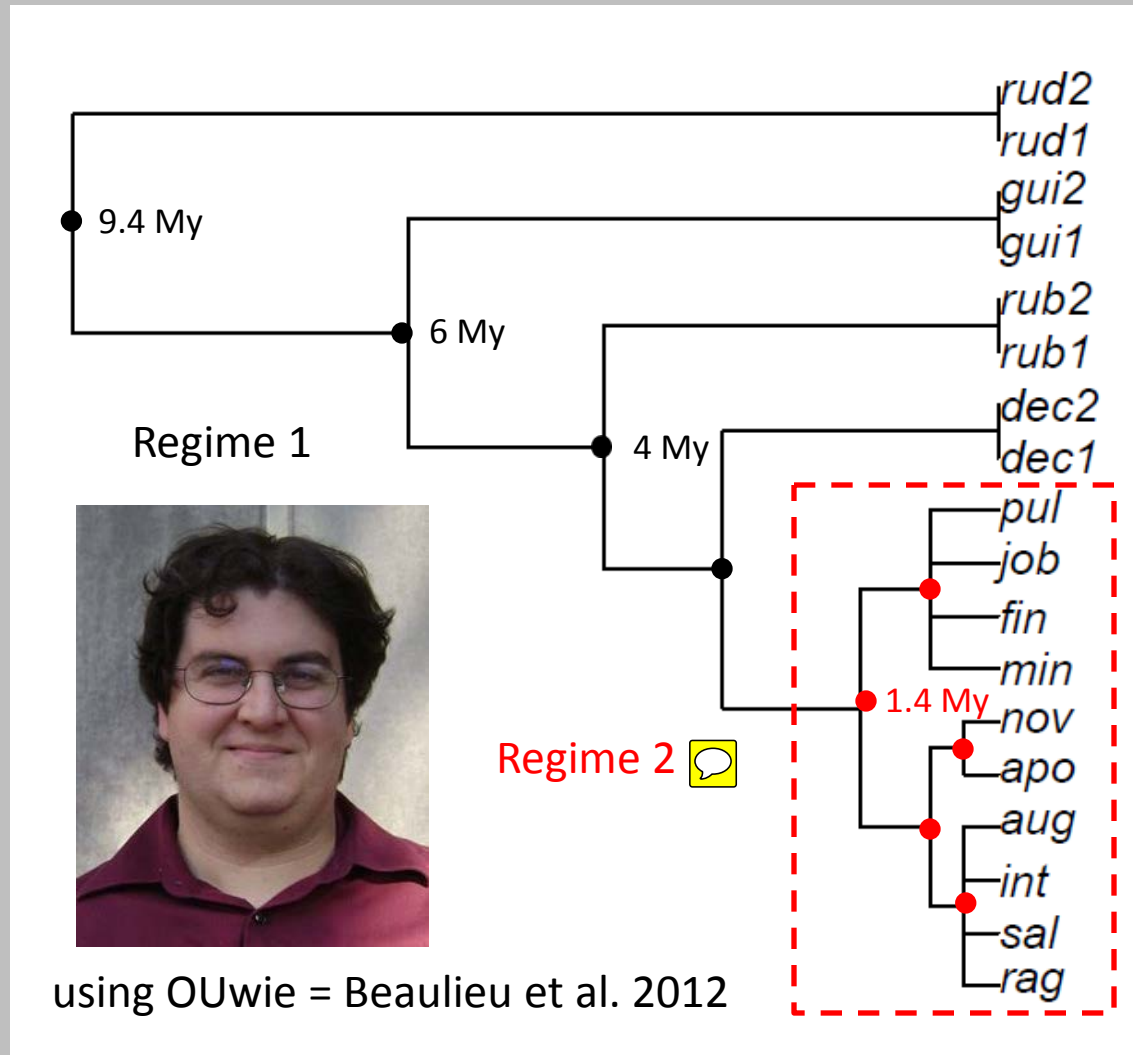


OU -> bounded evolution





Two versions: genetic drift or Brownian motion of peak

Tree for the genus *Paradisaea*: two hypothetical selection regimes





*Tests of alternative **generic models**: using generic BM & OU parameters in **OUwie***

Table 3. Comparison of Brownian Motion and Ornstein-Uhlenbeck model fits			
model	ΔAIC_c	Regime 1	Regime 2
BMS	0.00	$\sigma^2 = 3.18$	 $\sigma^2 = 110.81$
OUM	1.11	$\sigma^2 = 443.51, \theta = 52.60, \alpha = 12.49$	$\sigma^2 = 443.51, \theta = 59.29, \alpha = 12.49$ 
OU1	3.80	$\sigma^2 = 165.39, \theta = 55.13, \alpha = 3.14$	
BM1	6.08	$\sigma^2 = 72.42$	



σ^2 = stochastic diversification rate = increase in among-lineage
variance in trait means per 200,000 generations

θ = phenotypic optimum

α = restoring force, the rubber band in the OU process

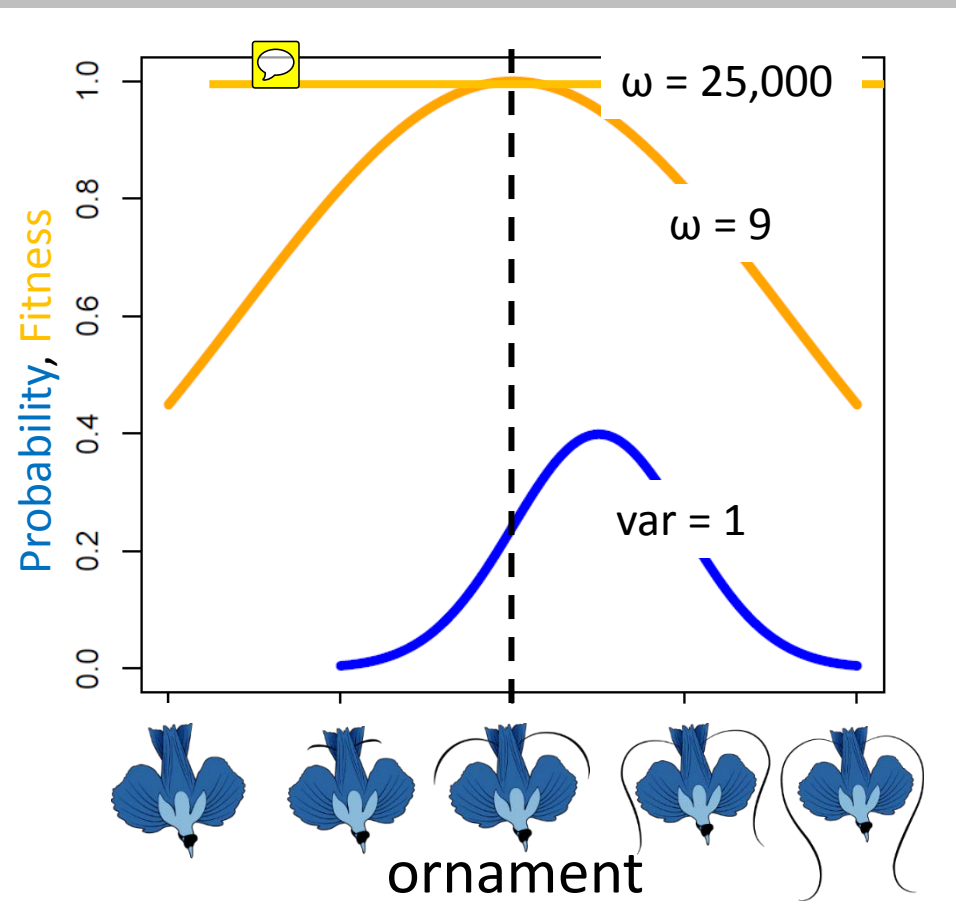
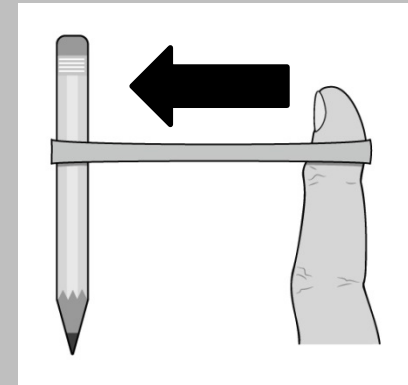


*Tests of alternative **generic models**: using quantitative genetic parameters*

Table 4. Comparison of Brownian Motion and Ornstein-Uhlenbeck model fits			
model	AICc	Regime 1	Regime 2
BMS	0.00	$N_e = 25,157; var_{\theta} = 0.000016$	 $N_e = 722; var_{\theta} = 0.00055$
OUM	1.11	$\omega = 6,404$	
OU1	3.80	 $\omega = 25,477$	
BM1	6.08	$N_e = 1,105; var_{\theta} = 0.00036$	

Under the genetic drift interpretation of BM, $\sigma^2 = tG/N_e$, solve for N_e ; or under moving optimum interpretation of BM, $\sigma^2 = t var_{\theta}$, solve for var_{θ} .
Using the OU models, solve $\alpha = tG/(\omega + P)$ for ω = width of fitness function, analogous to a variance.

Visualizing very weak stabilizing selection



Conclusion using **generic models** (OUwie): need moving peaks

- Brownian motion of a natural selection optimum for preferences is the best-fitting and most plausible model for the data.
- This conclusion is consistent with results using the Phenotypic Tango model.
- BM of an intermediate optimum may be a reasonable model for adaptive radiations in general.

The Future

- Need solution for Phenotypic Tango model
- Need a version of the model that includes peak movement
- Need better data and more of it
- Need testing framework for model that incorporates prior information and estimates multivariate quantitative genetic parameters



Uyeda & Harmon 2014



Acknowledgements

NESCent/NIMBioS Course in Evolutionary Quantitative Genetics:

Joe Felsenstein = co-organizer; with Patrick Carter, Patrick Phillips, Adam Jones, Trudy Mackay, Marguerite Butler, Emilia Martins, Paul Hohenlohe, Liam Revell, Brian O'Meara, Luke Harmon, Michael Whitlock, Josef Uyeda, Tyler Heather, Matt Pennell = guest instructors.



Illustrations:
Ivan Phillipsen

References

- Arnold, S. J. & L. D. Houck. 2016. Can the Fisher-Lande process account for birds of paradise and other sexual radiations. *American Naturalist* 187:000-000.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon, London.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Nat. Acad. Sci. USA* 78:3721–3725.
- LeCroy, M. 1981. The genus *Paradisaea* - display and evolution. *American Museum Novitates* 2714: 1-52.
- Irestedt, M., K. A. Jønsson, J. Fjeldså, L. Christidis and P. G. P. Ericson. 2009. An unexpectedly long history of sexual selection in birds-of-paradise. *BMC Evolutionary Biology* 9, No. 235.
- Beaulieu, J. M., D.-C. Jhwueng, C. Boettiger, and B. C. O'Meara. 2012. Modeling stabilizing selection: Expanding the Ornstein-Uhlenbeck model of adaptive evolution. *Evolution* 66: 2369-2383.