# Cross-lags, heterogeneity, and life-history trade-offs

**No class on Thursday (the 10th)**

**Today is another fun paradox day!**

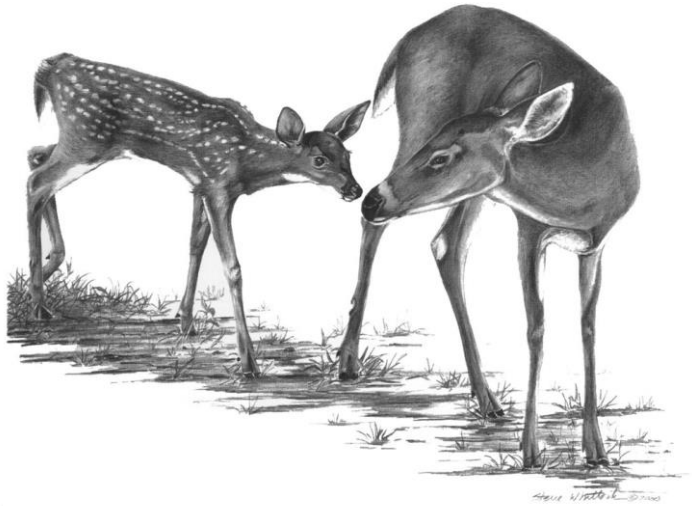
# Today we’re going to follow 100 female gators around for 7 years

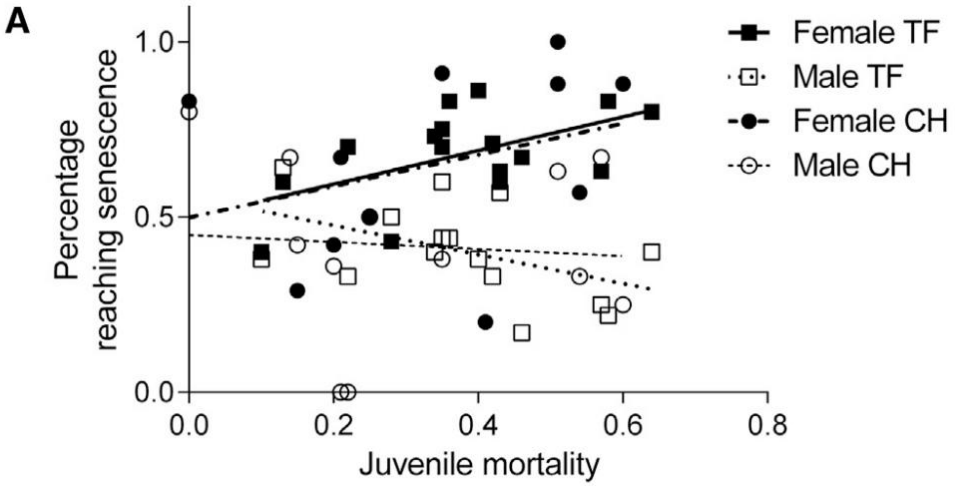

We’ll mark individuals, capture them prior to each breeding season to record morphometric data, and visit their nests to measure fecundity.

# Female alligators provide parental care

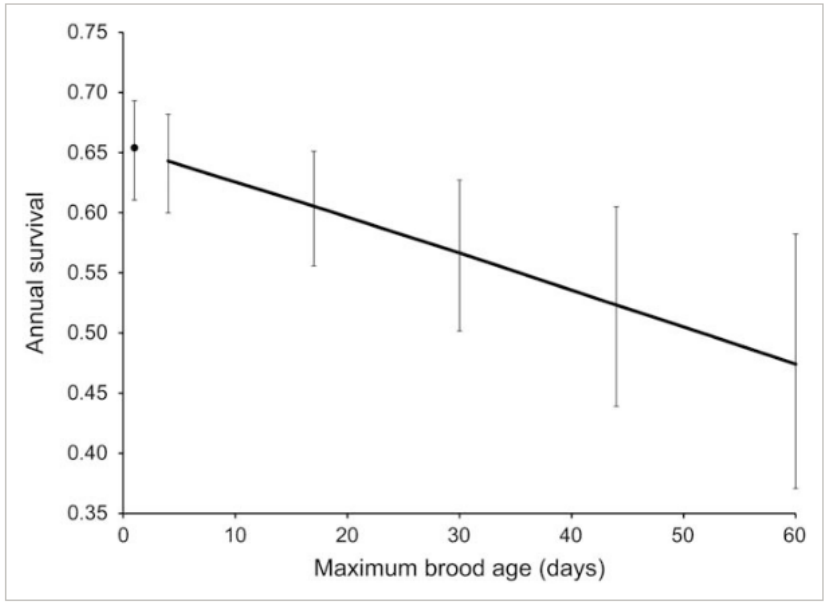

# We'll imagine there's a cost to that (i.e., trade-off)

# Life-history trade-offs



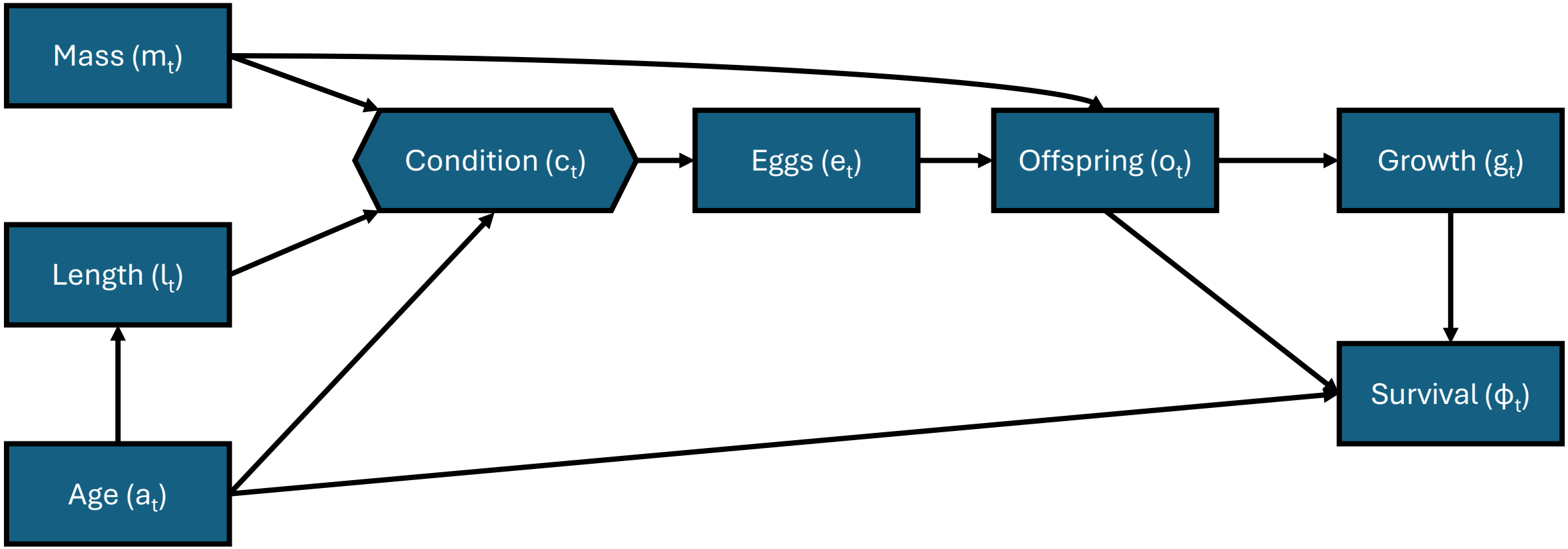



Garratt et al. (2015) Current Biology




Arnold and Howerter (2012) Wildlife Society Bulletin

# We could imagine a wildly complicated model here!?




Bühler, Riecke, et al. **(2024)** *Royal Society Open Science*
Layton-Matthews et al. **(2019)** *Global Change Biology*

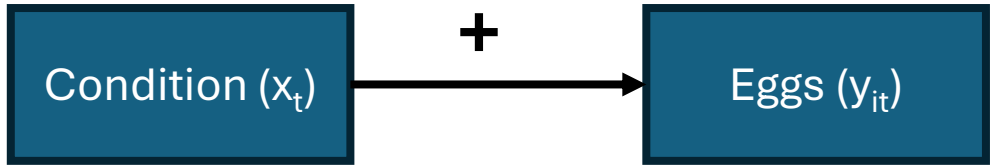
## But today we’ll measure just two traits

- Body condition (x; this will be centered)
- Clutch size (y; this will be measured in eggs)

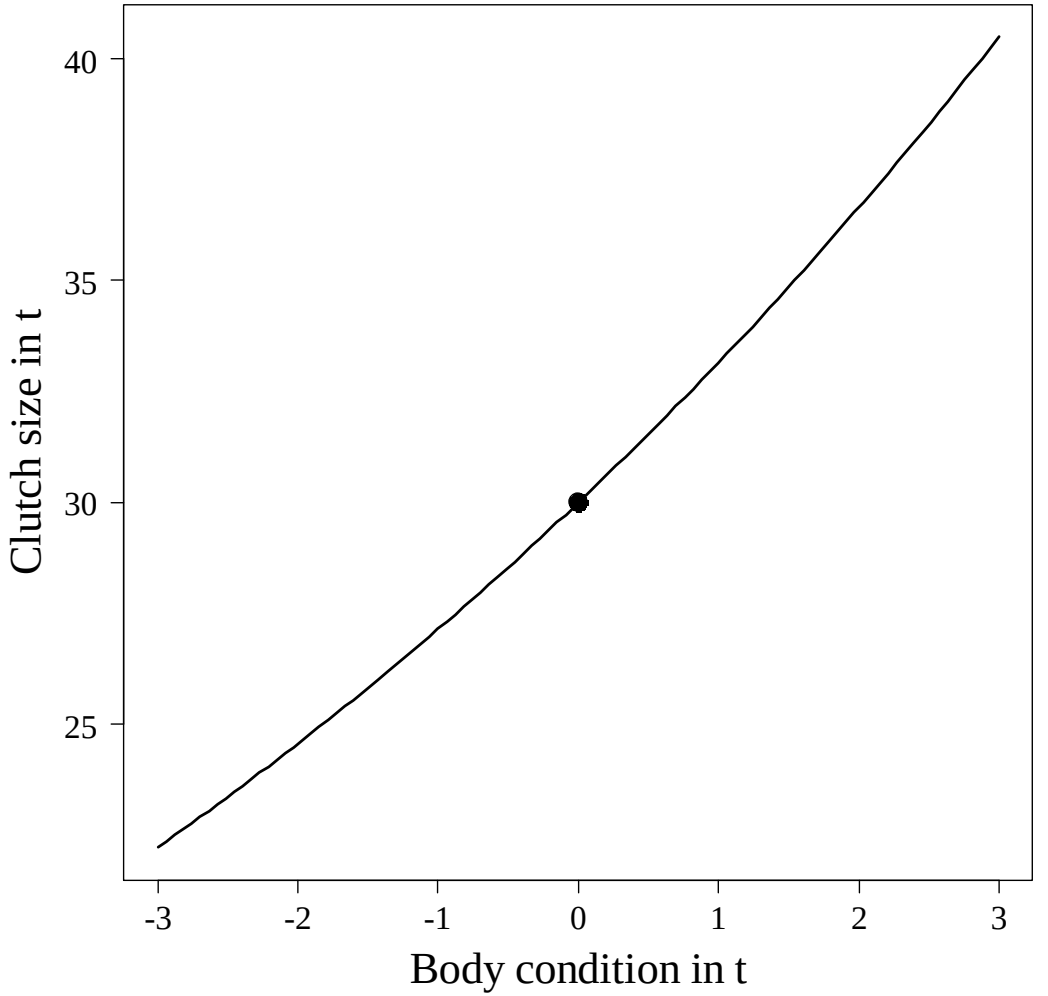
# Body condition (x; centered, i.e., μ = 0)

# Clutch size (y; number of eggs)

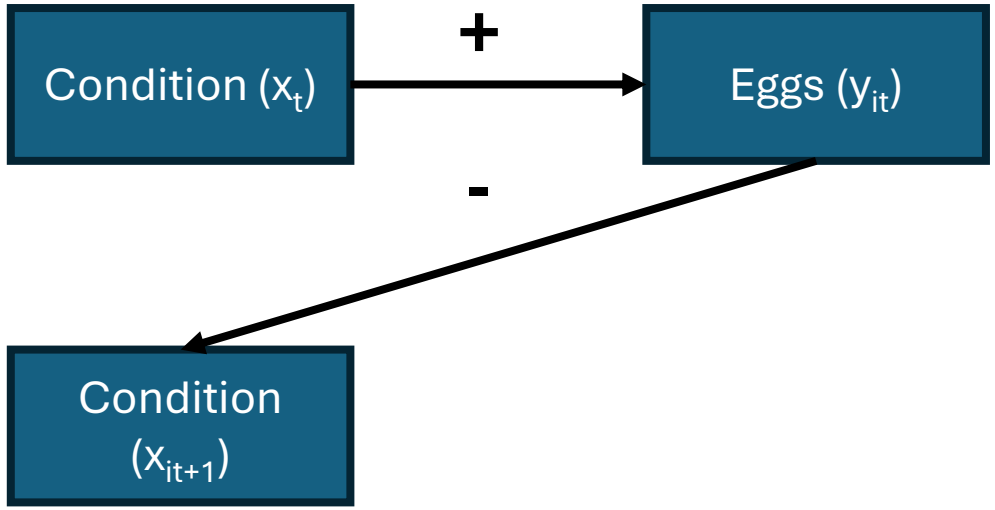
# Hypothesis 1: Alligators in better condition will lay more eggs




$$y_{it} \sim \text{Poisson}(e^{\alpha_{i1} + \beta_1 x_{it}})$$

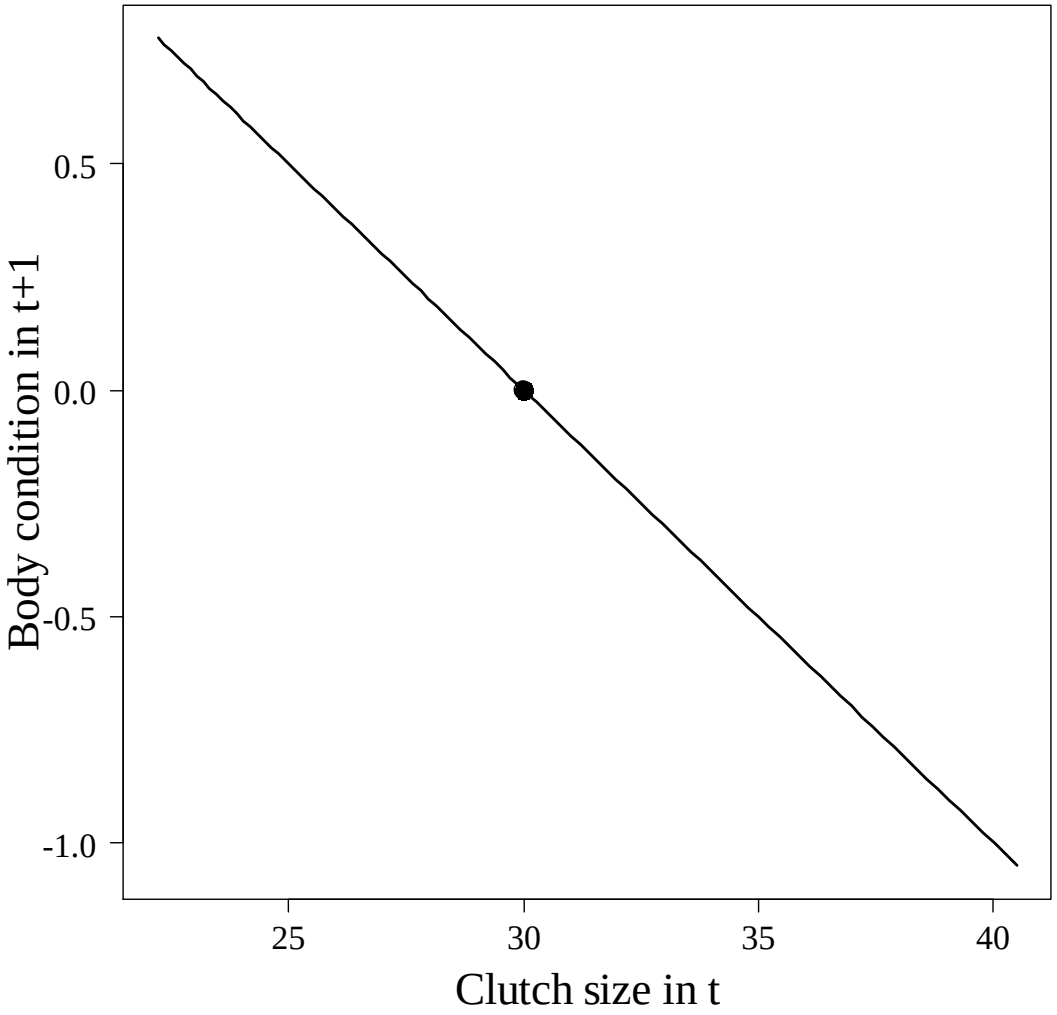


# Hypothesis 2: Alligators that lay more eggs will ‘lose’ condition

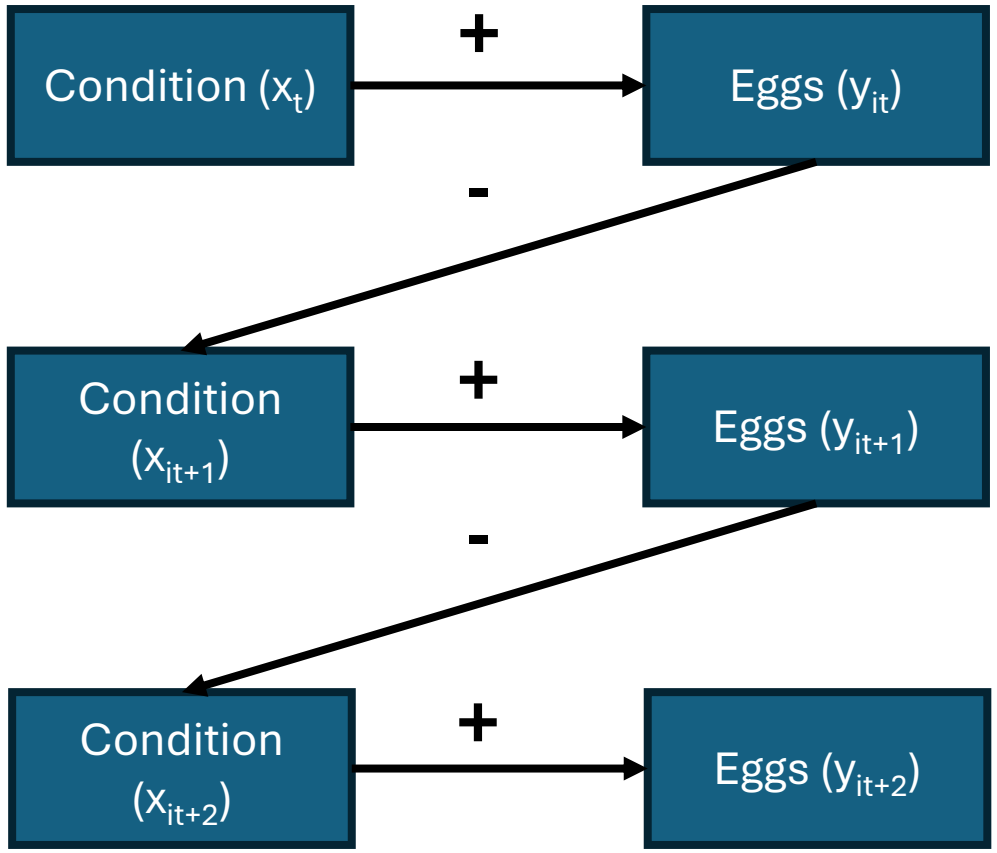


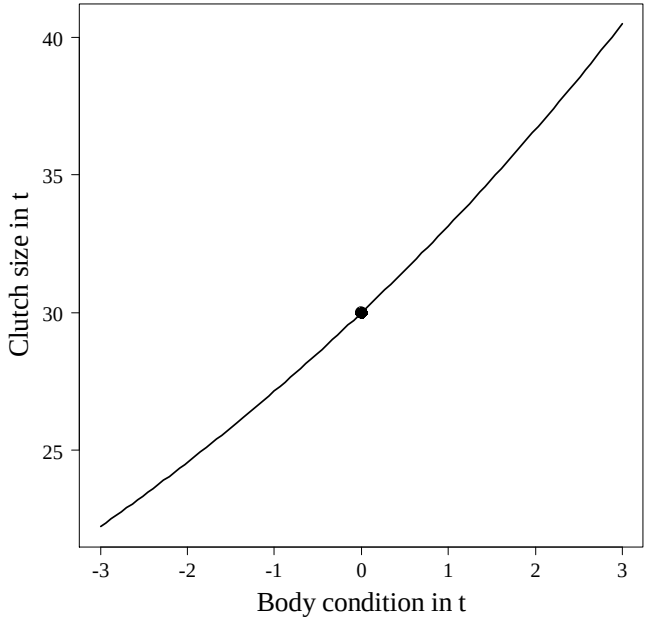

$$E(x_{it+1}) = \alpha_{i2} + \beta_2 \times (y_{it} - e^{\alpha_{i1}})$$

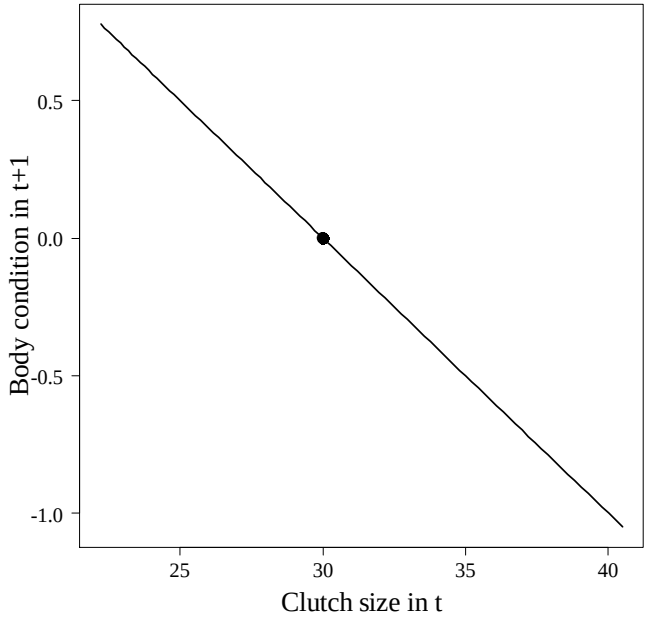
$$x_{it+1} \sim \text{Normal}(E(x_{it+1}), \sigma_x^2)$$



# And so on and so forth…

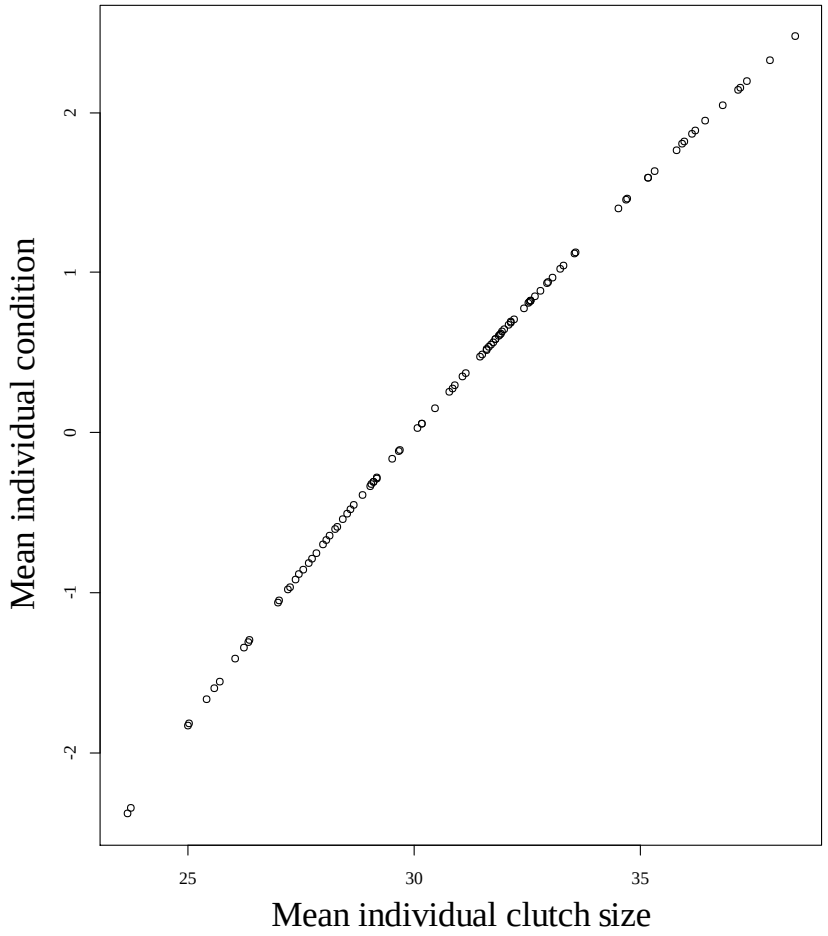


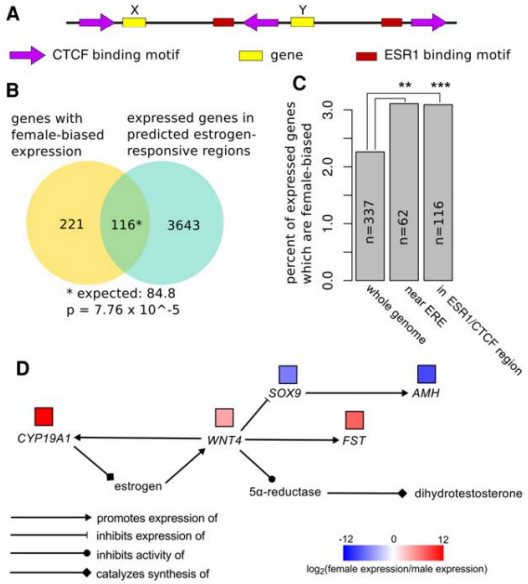



# There’s one ‘wrench’ in our plans

# The wrench: These alligators are different (i.e., heterogeneous)…

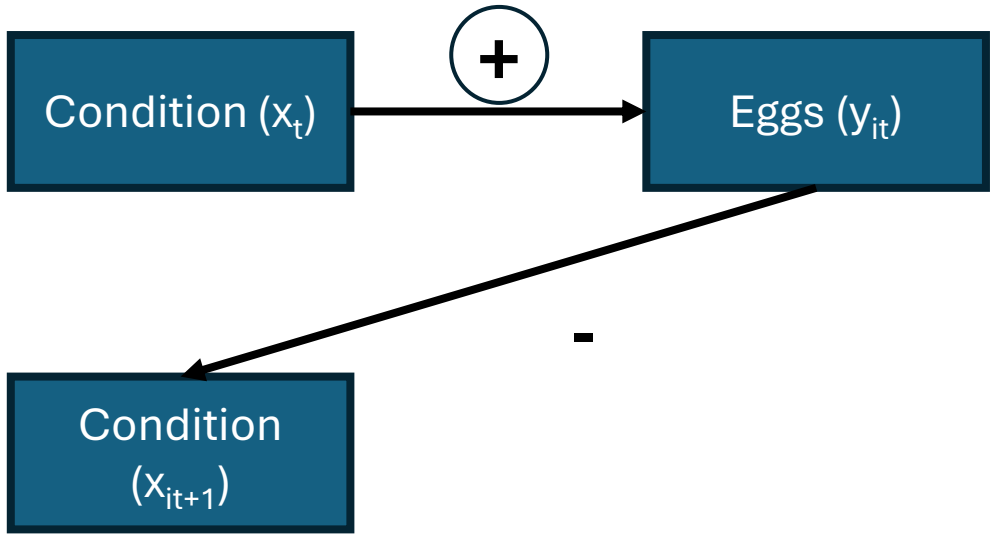


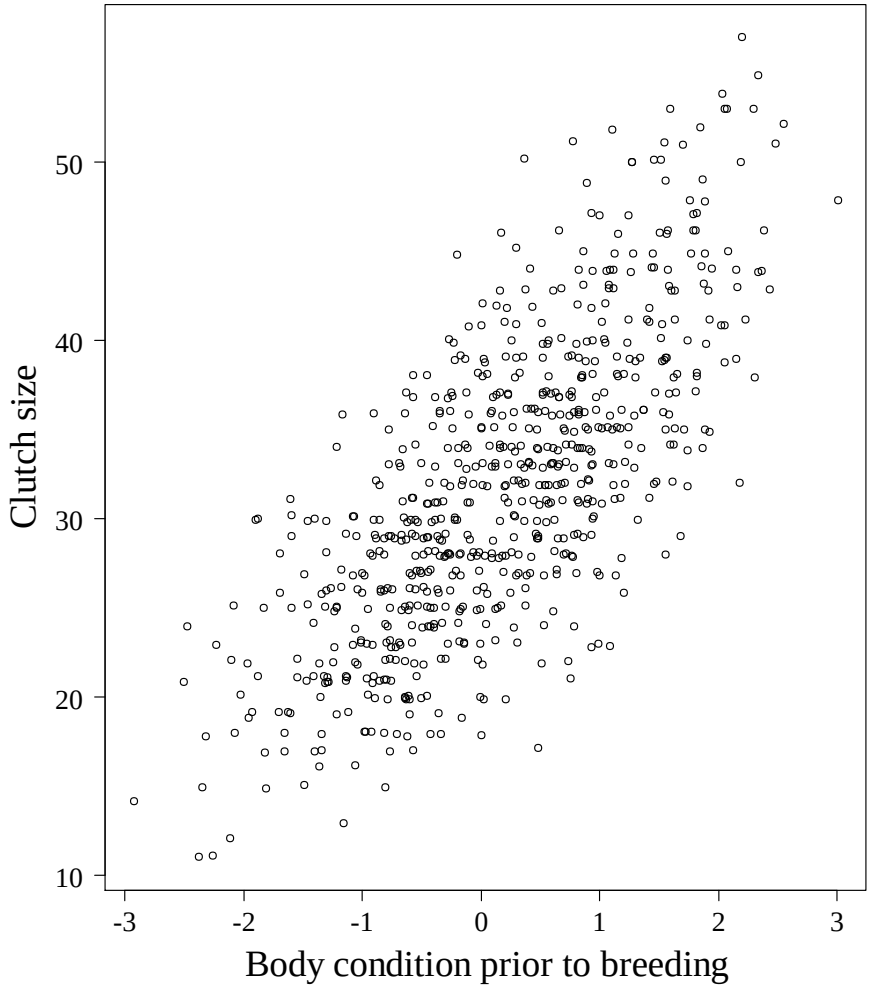




**This could be due to <u>unmeasured individual differences</u> or <u>territory quality</u>**

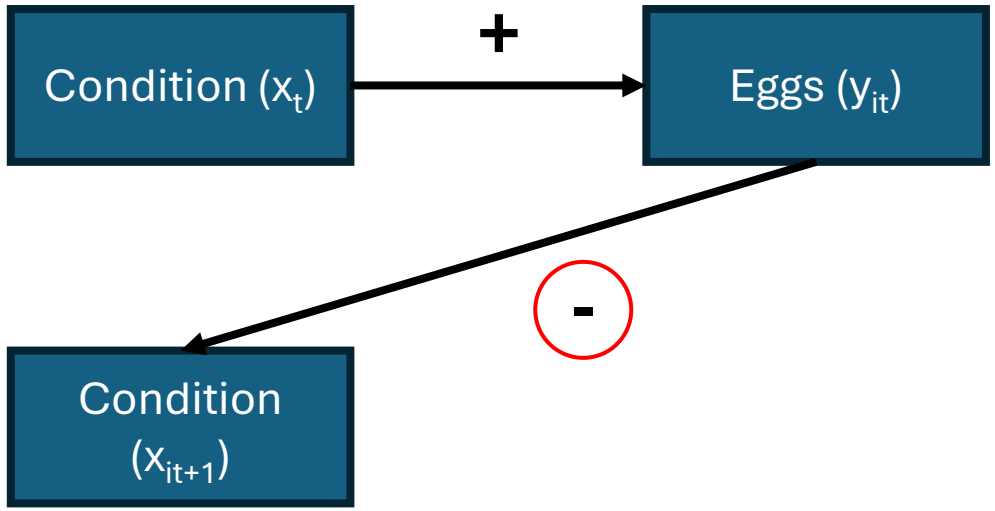
# So, what do we see at the population level?

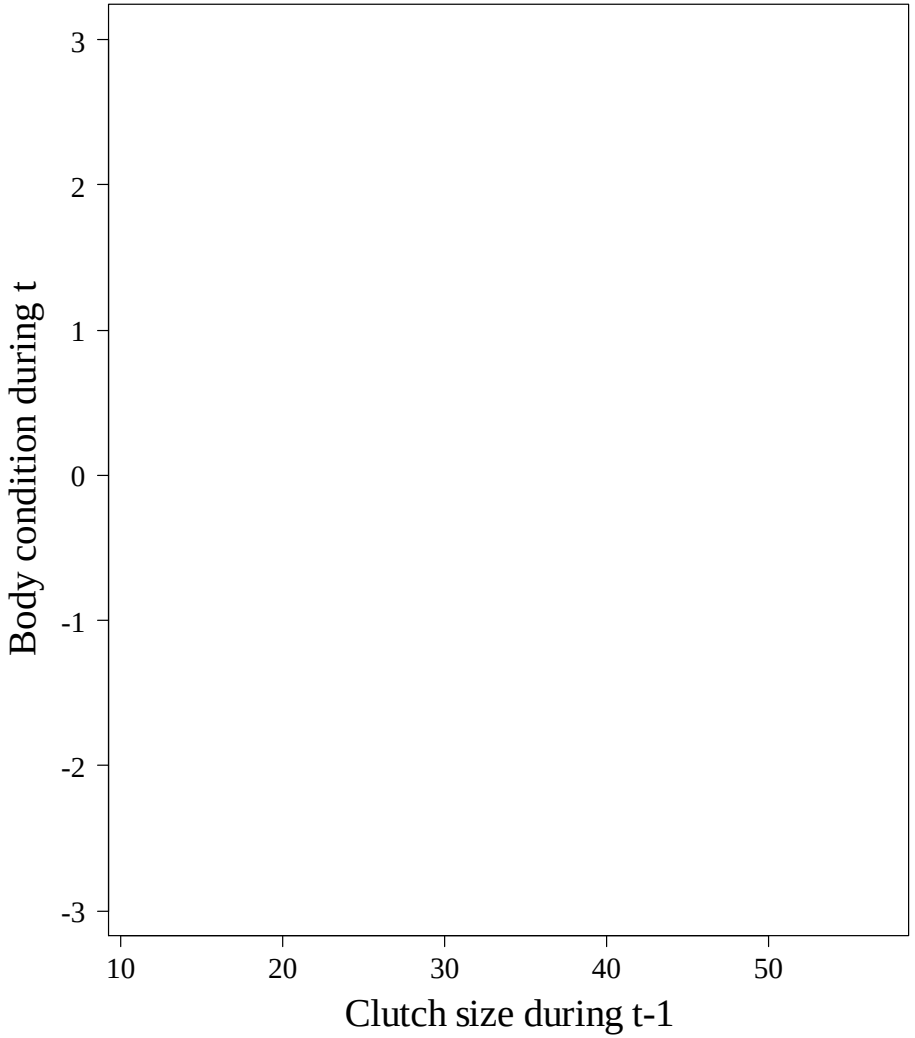
# Better condition leads to more eggs in a clutch



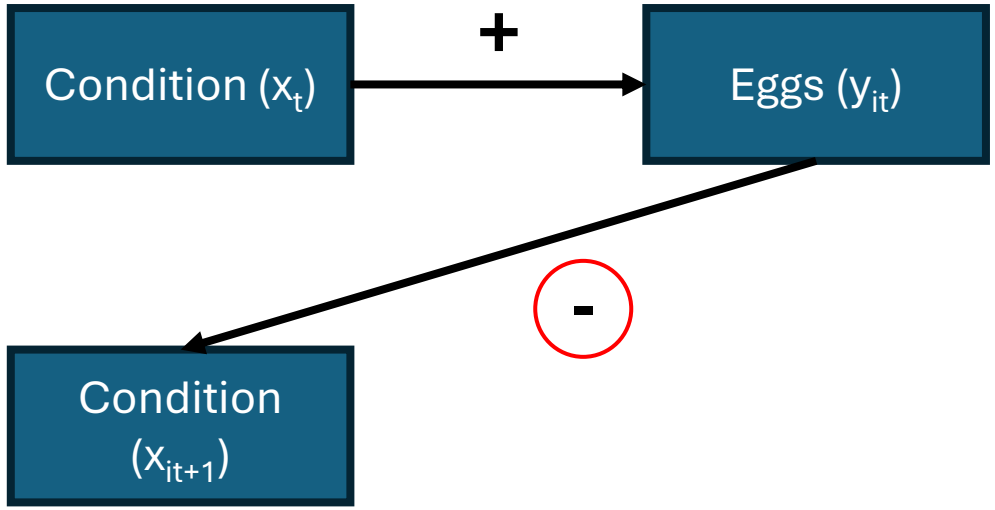



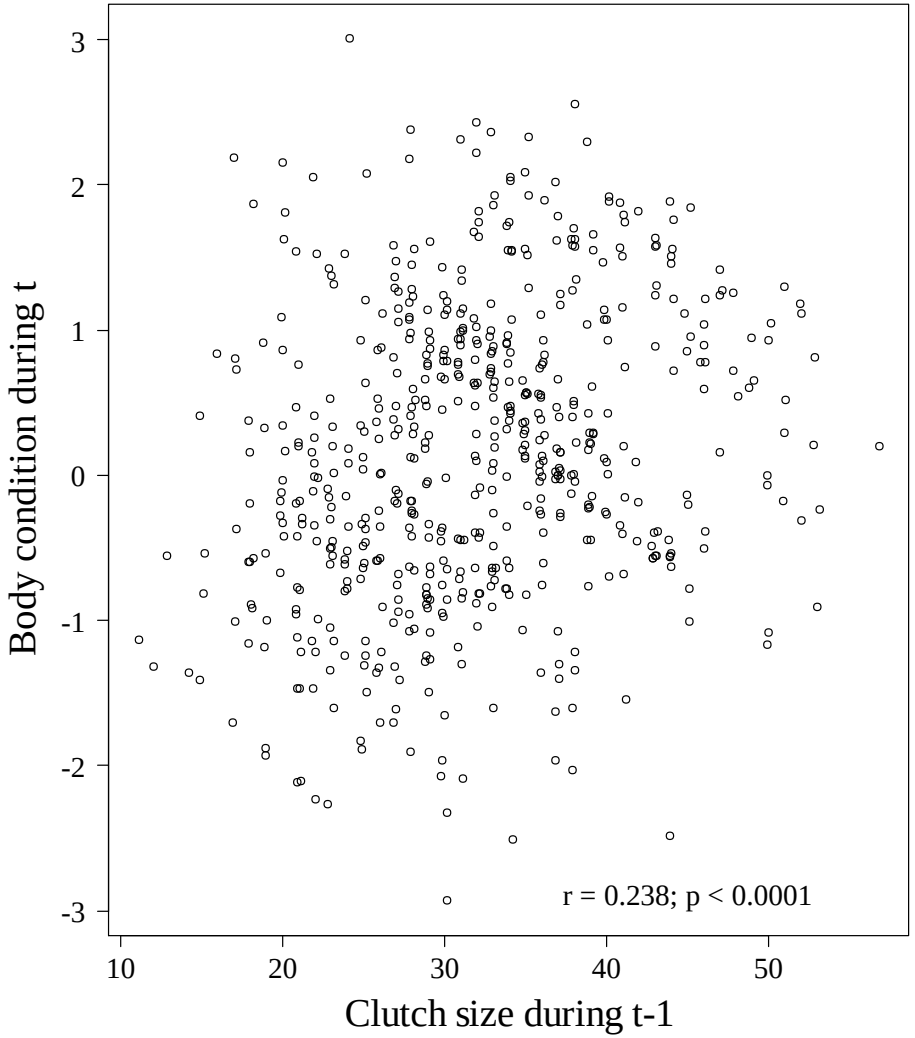
# Laying more eggs leads to…



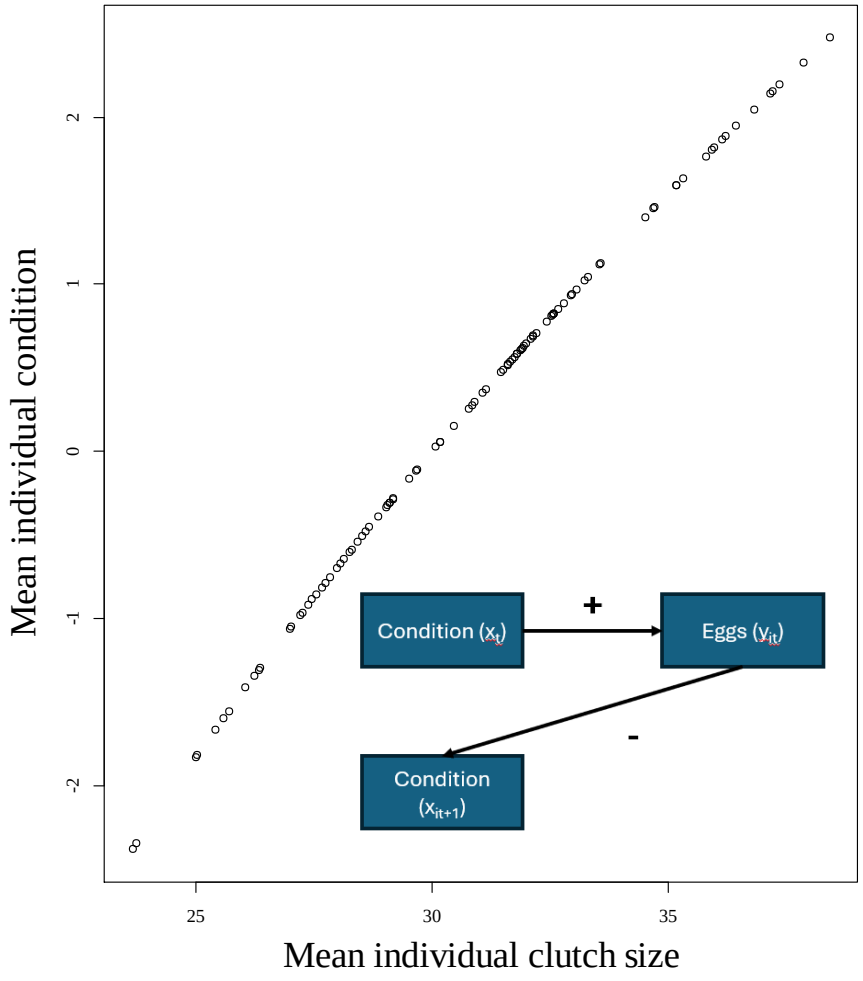
# Laying more eggs leads to… better condition next year?!

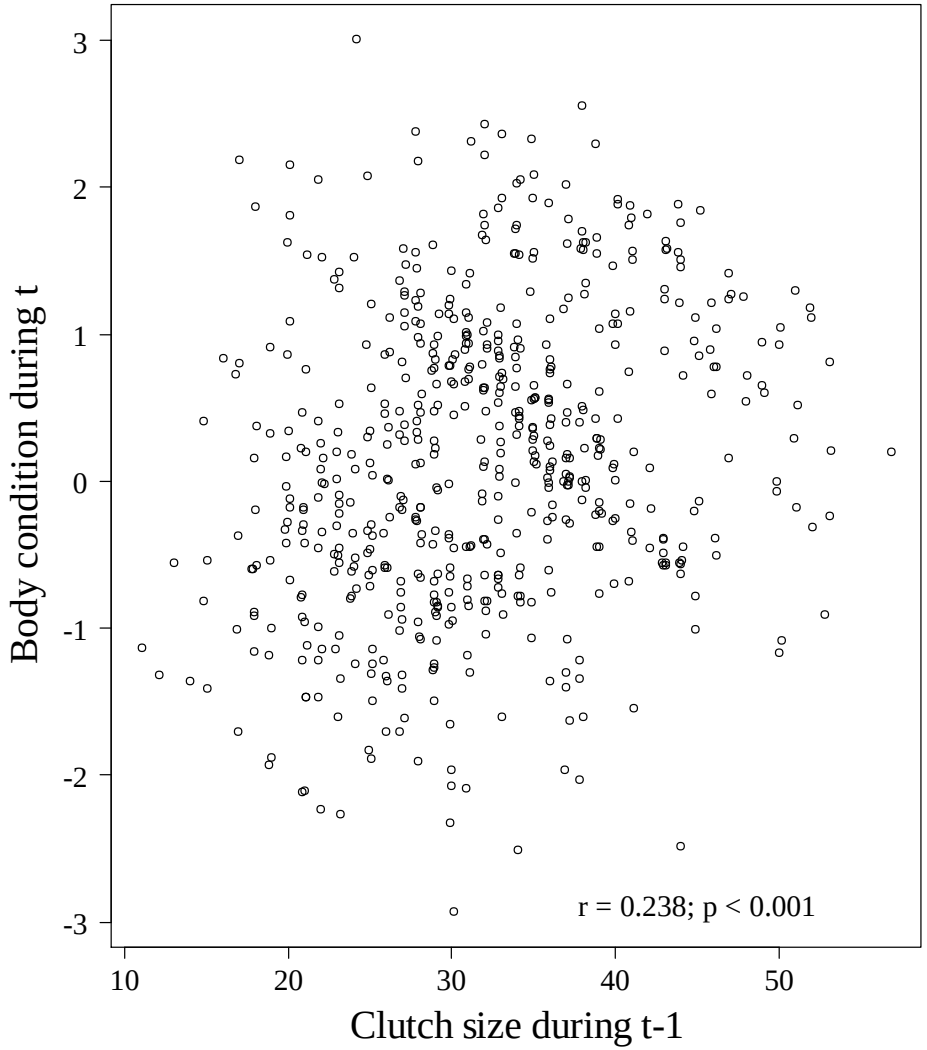



# What's happening here?

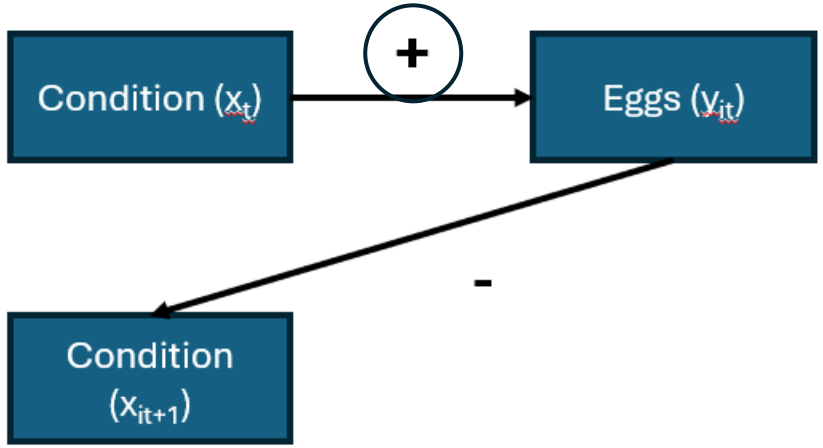
# What's happening here?!

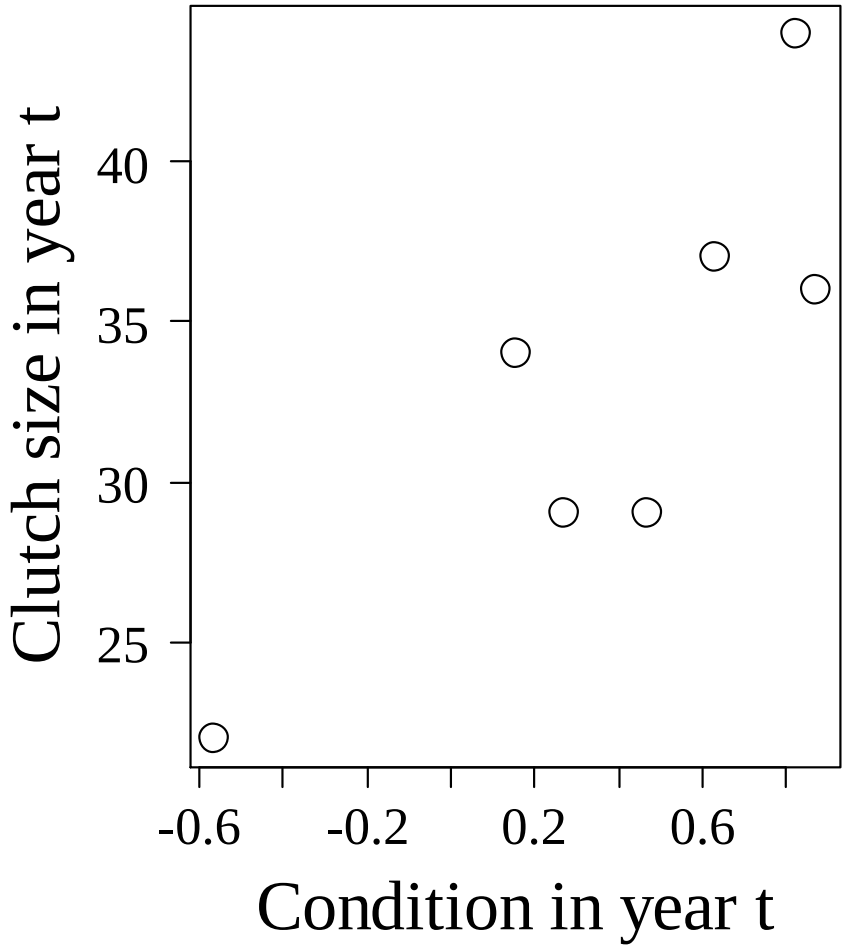



# Talk to your neighbor(s), look for patterns in the right-hand figure

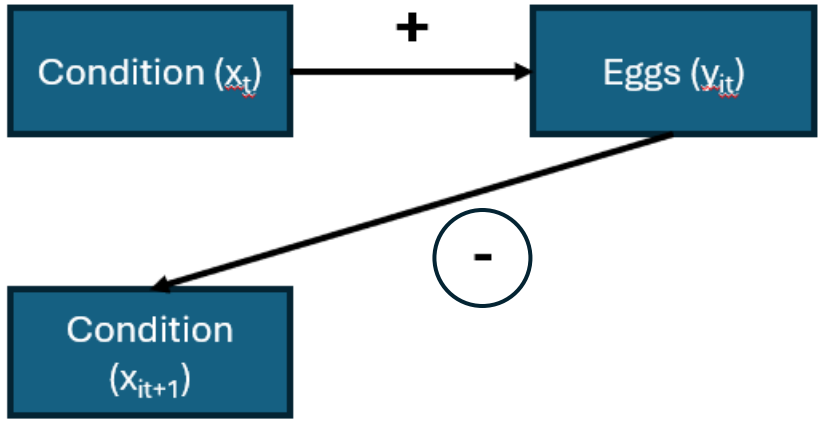
# What's happening here?! Let's look at an individual

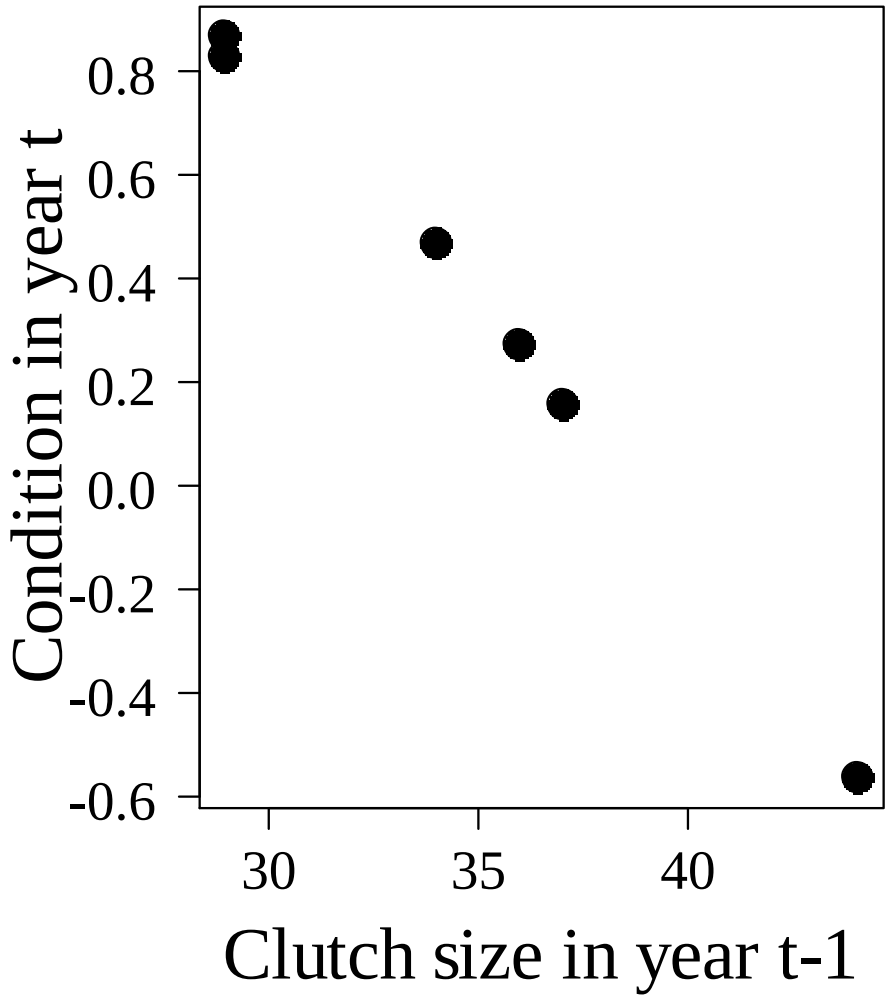



# Still a positive effect of condition on clutch size

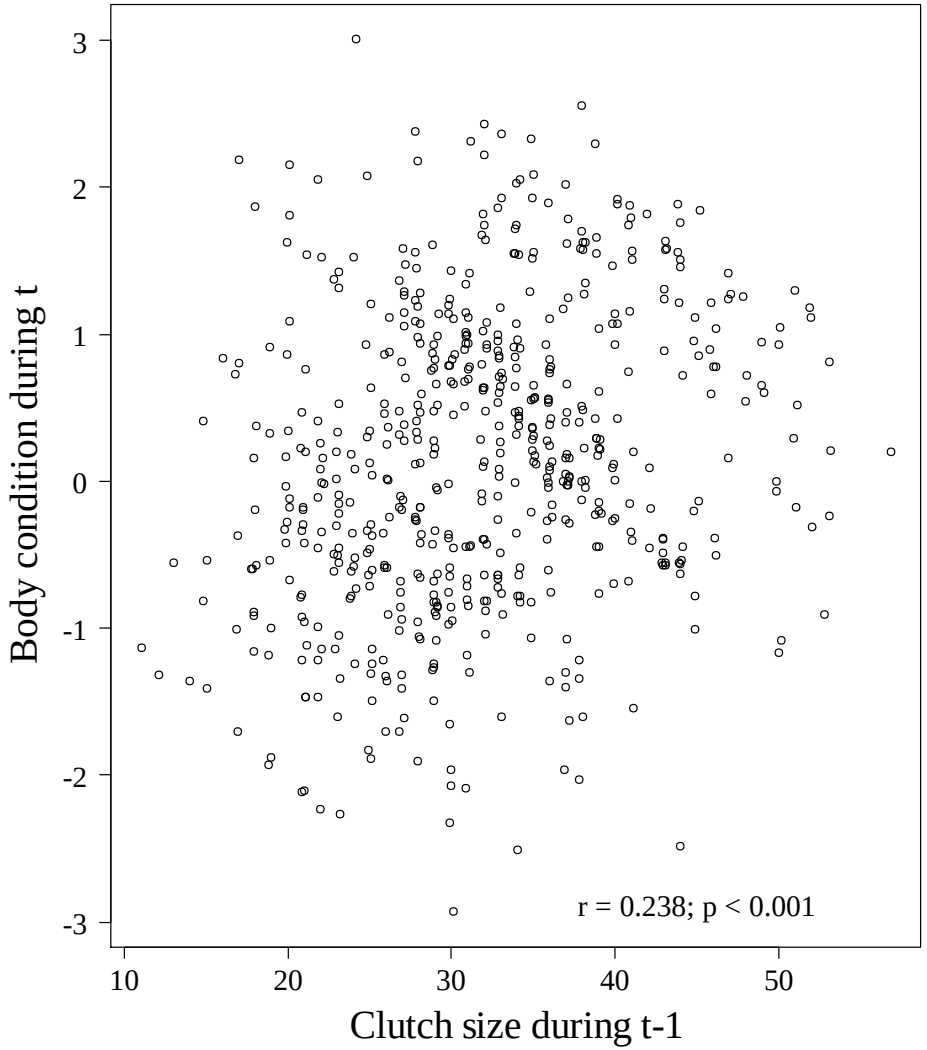
# What's happening here?! Let's look at an individual



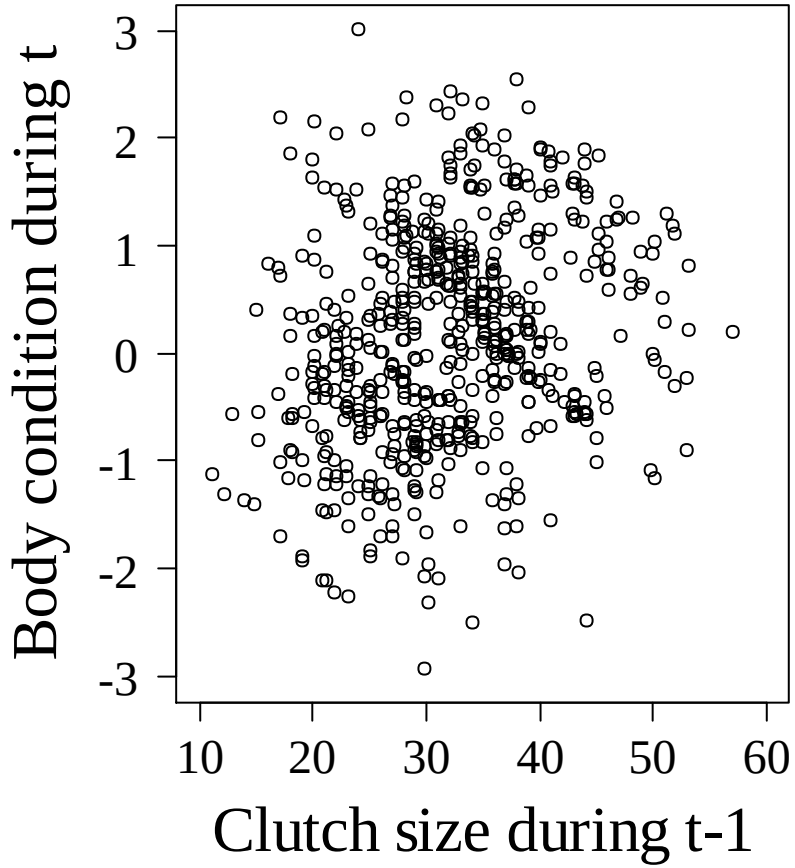



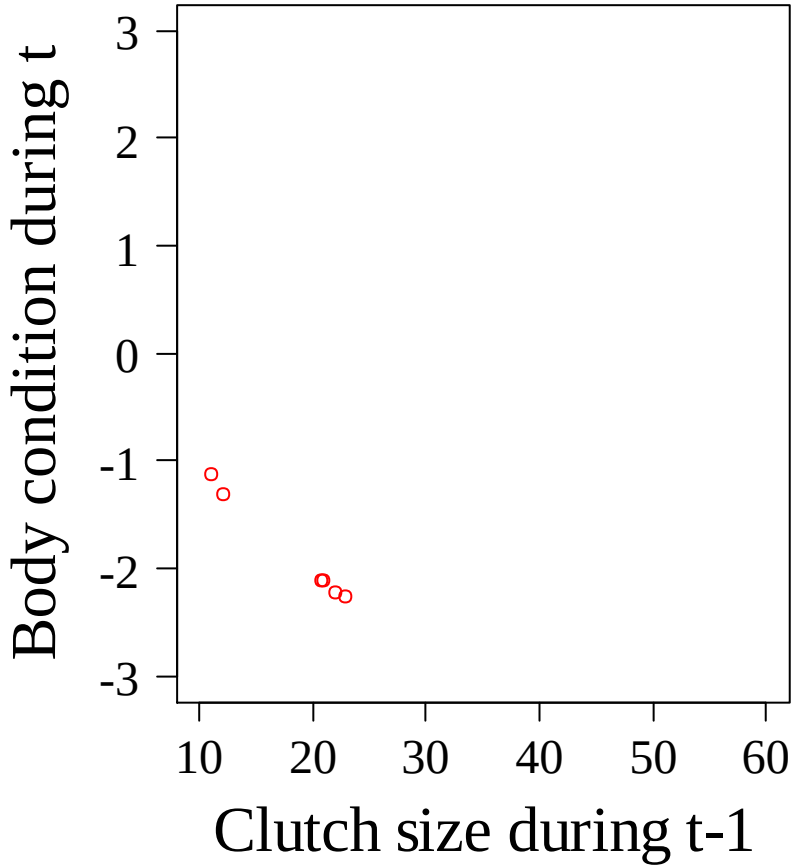

**Trade-offs are still happening (cost of reproductive investment)**

# What's happening here?!



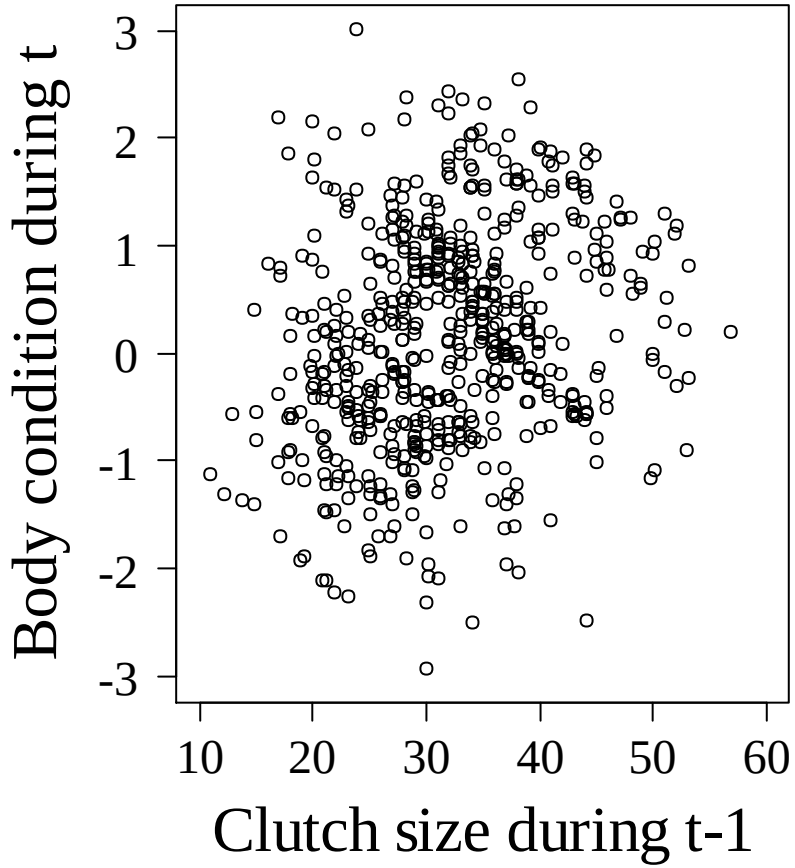
# What's happening here?!

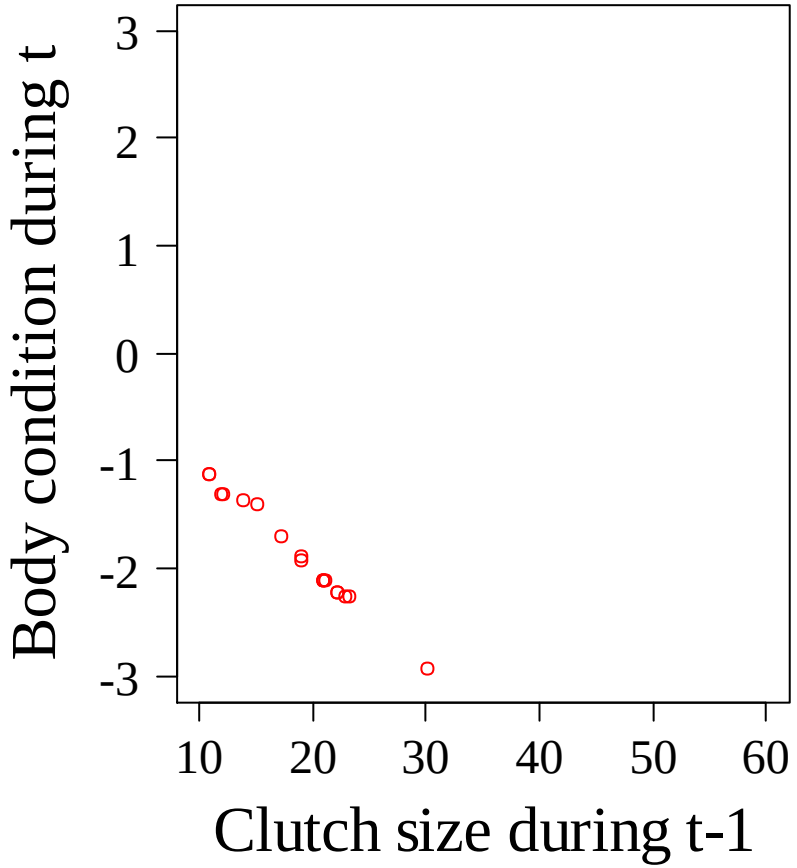



# Here is the 'worst' gator

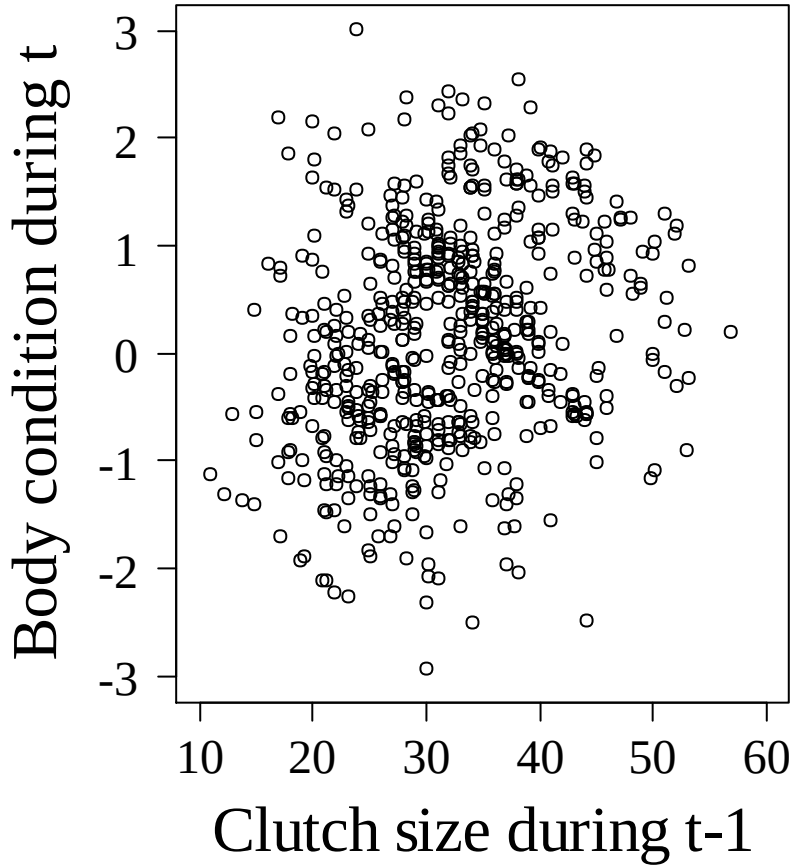
# What's happening here?!

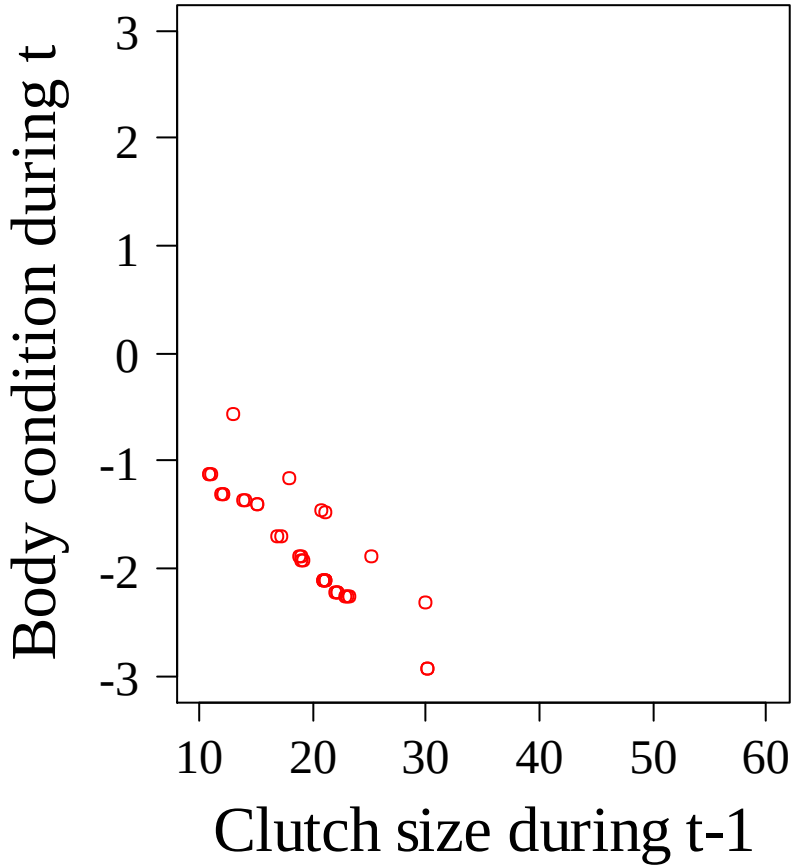



# Here are the two 'worst' gators

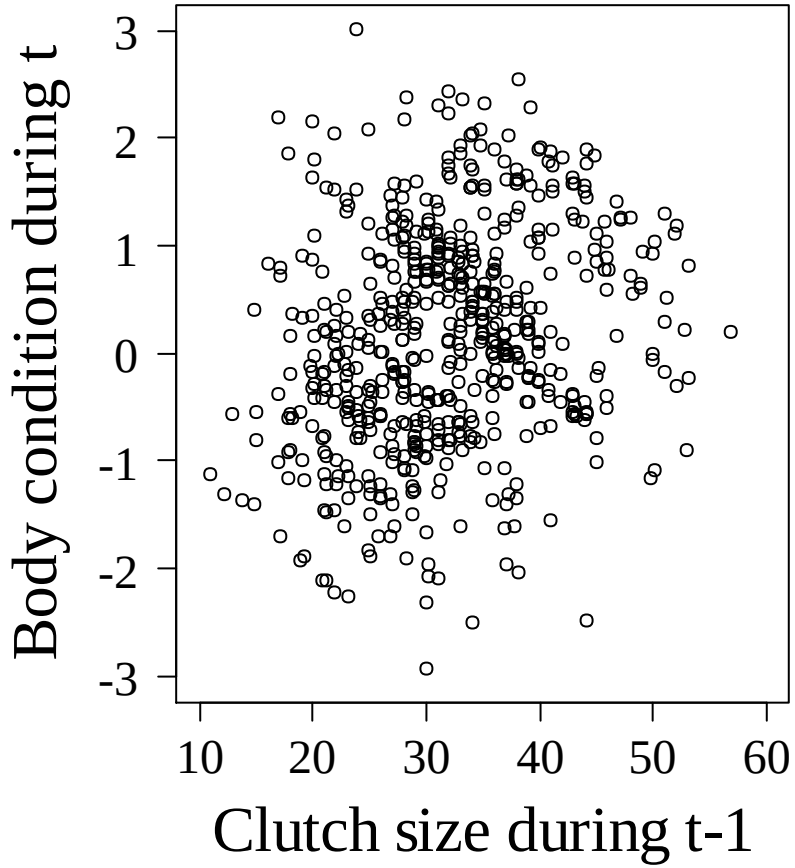
# What's happening here?!

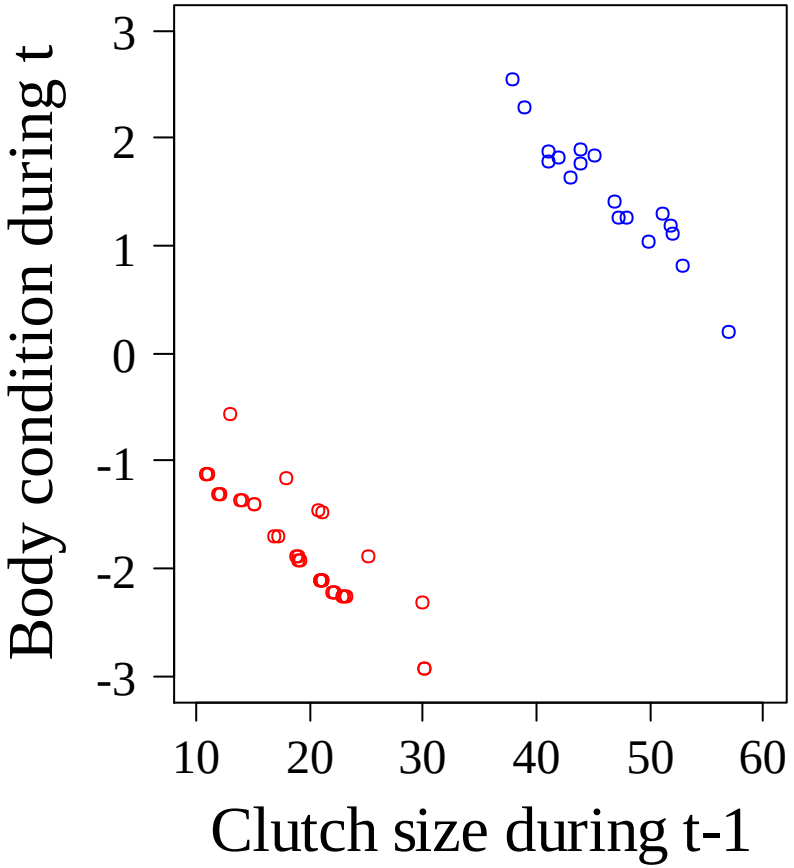



# Here are the three 'worst' gators

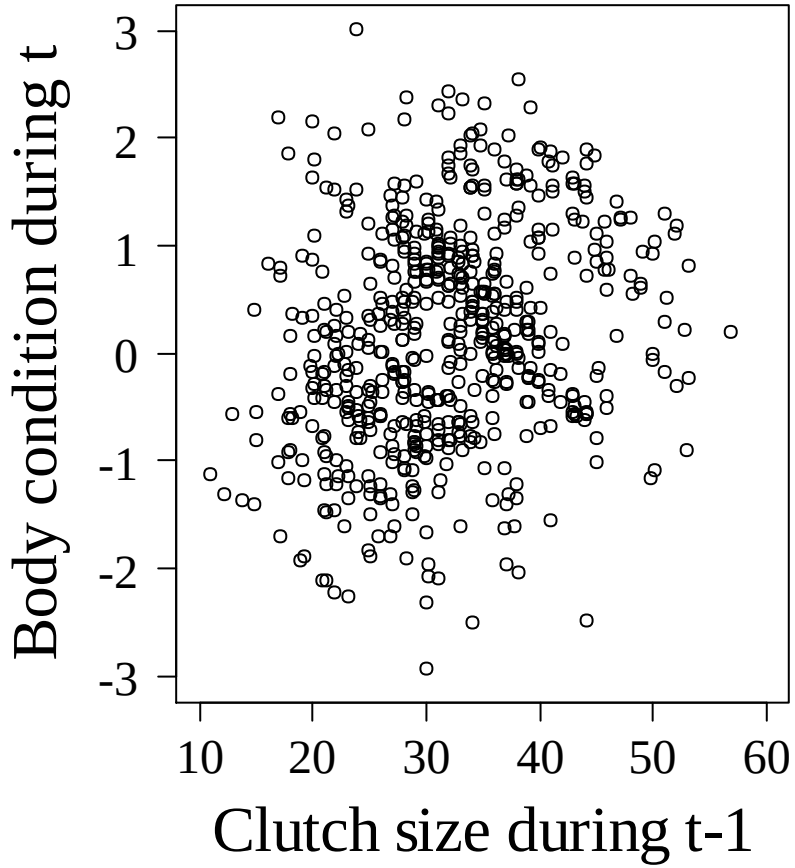
# What's happening here?!

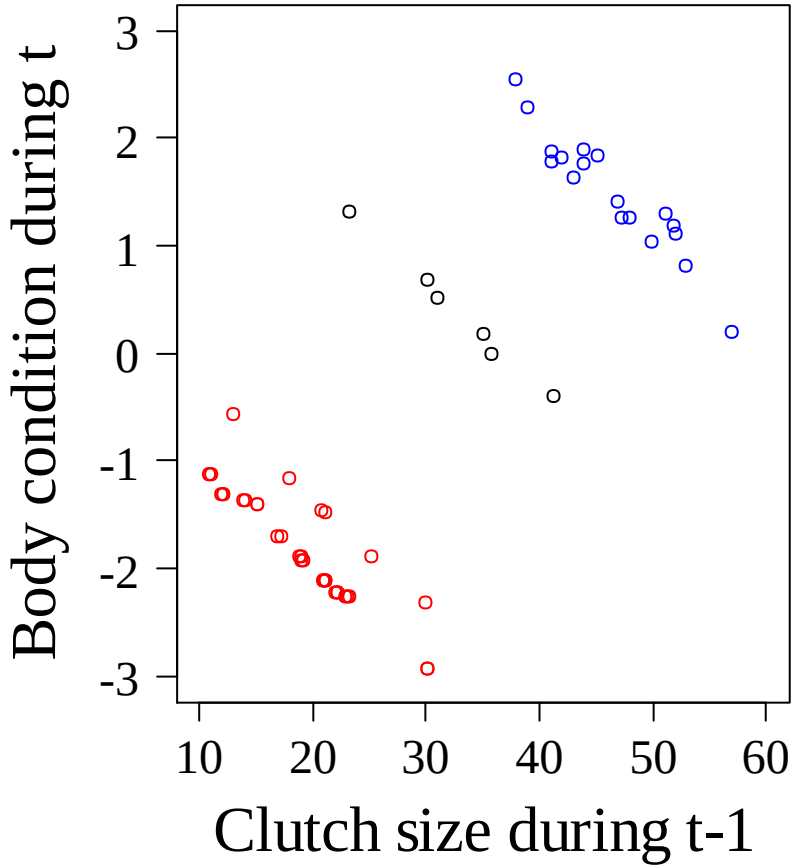



## Here are the three 'worst' and three 'best' gators

# What's happening here?!

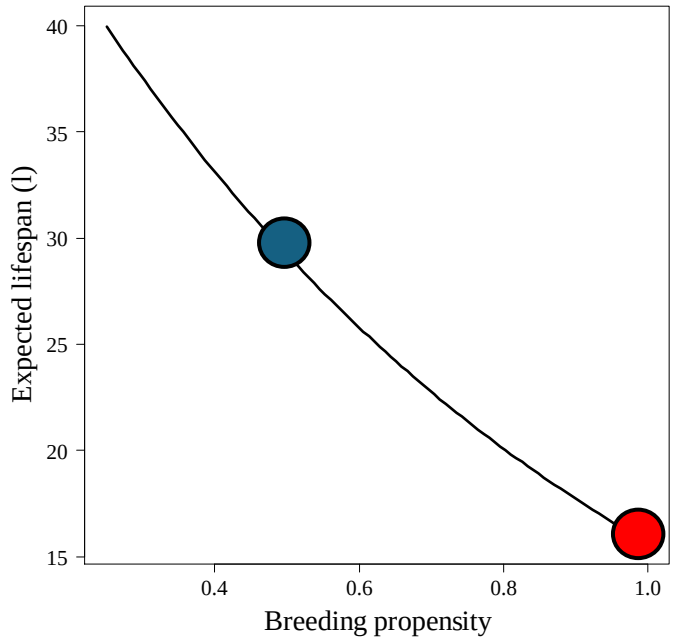


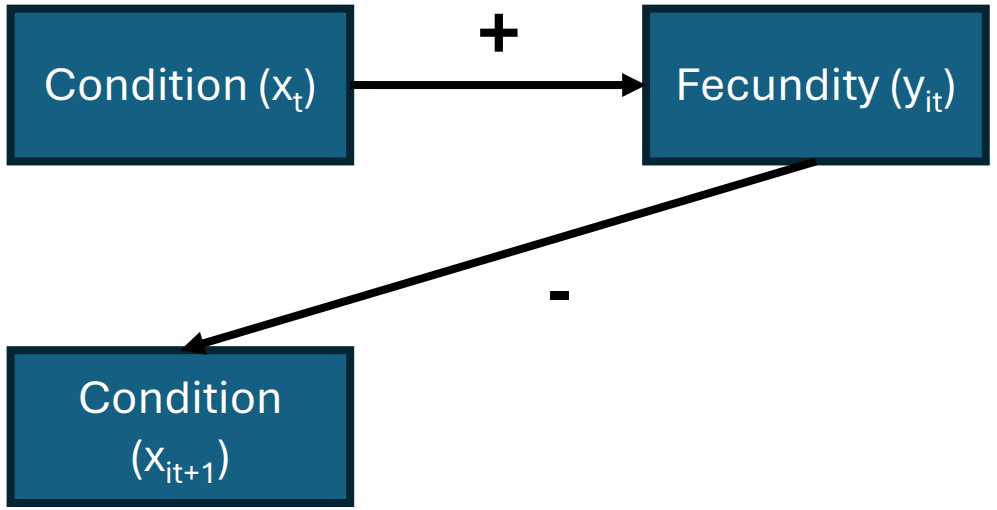




# Here are the three 'worst', three 'best', and median gators

# A real-life example: Laysan albatross

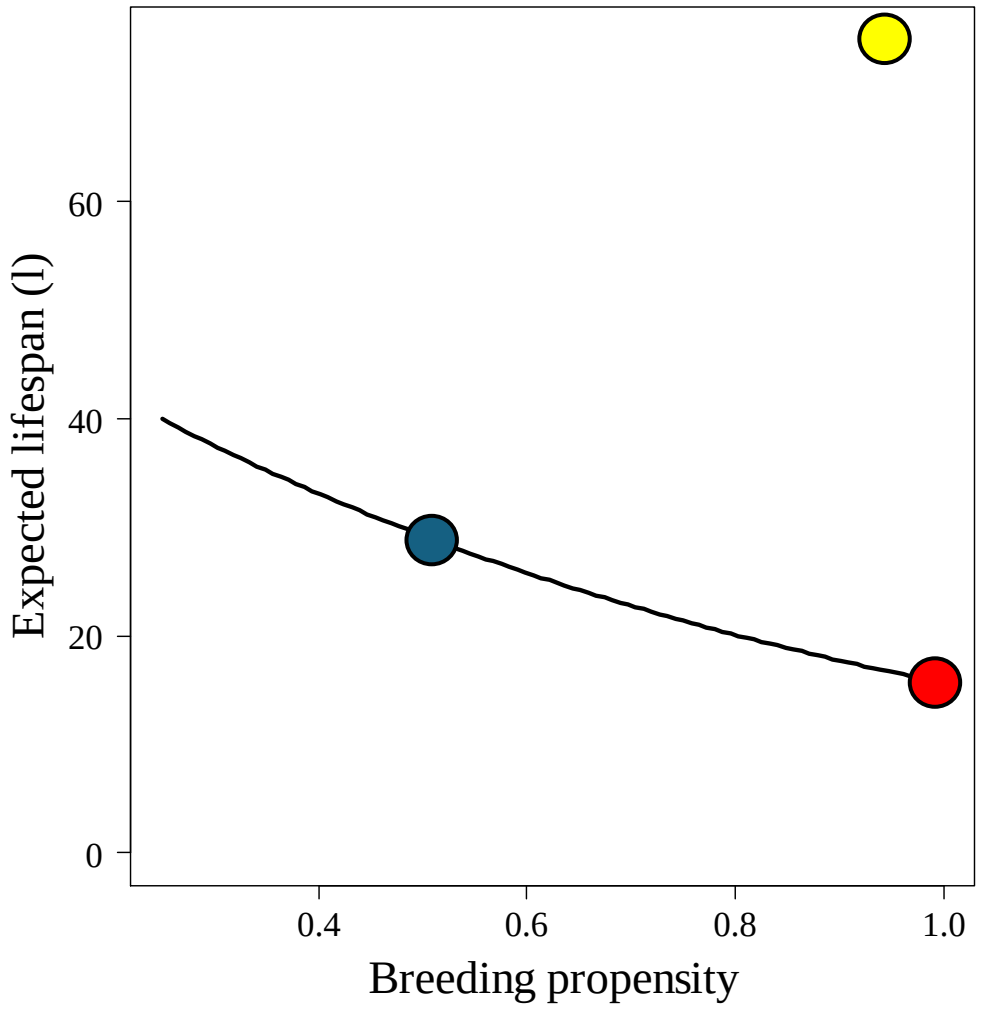
- Long-lived (30+ years)
- Delayed maturity (7-9 years)
- Lay a single egg
- Incubation (2 months)
- Fledging (5 months)



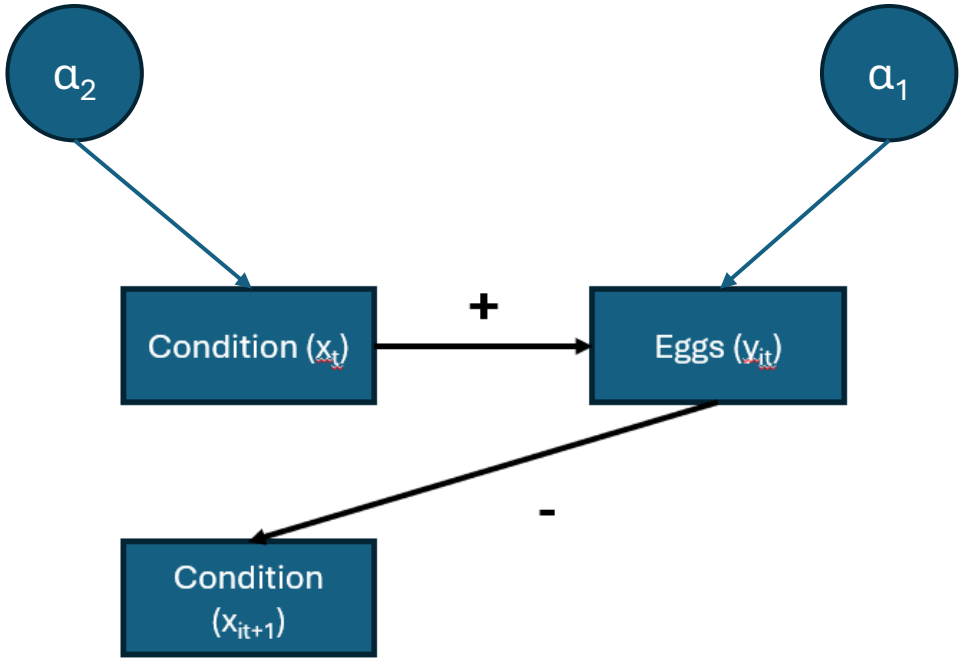



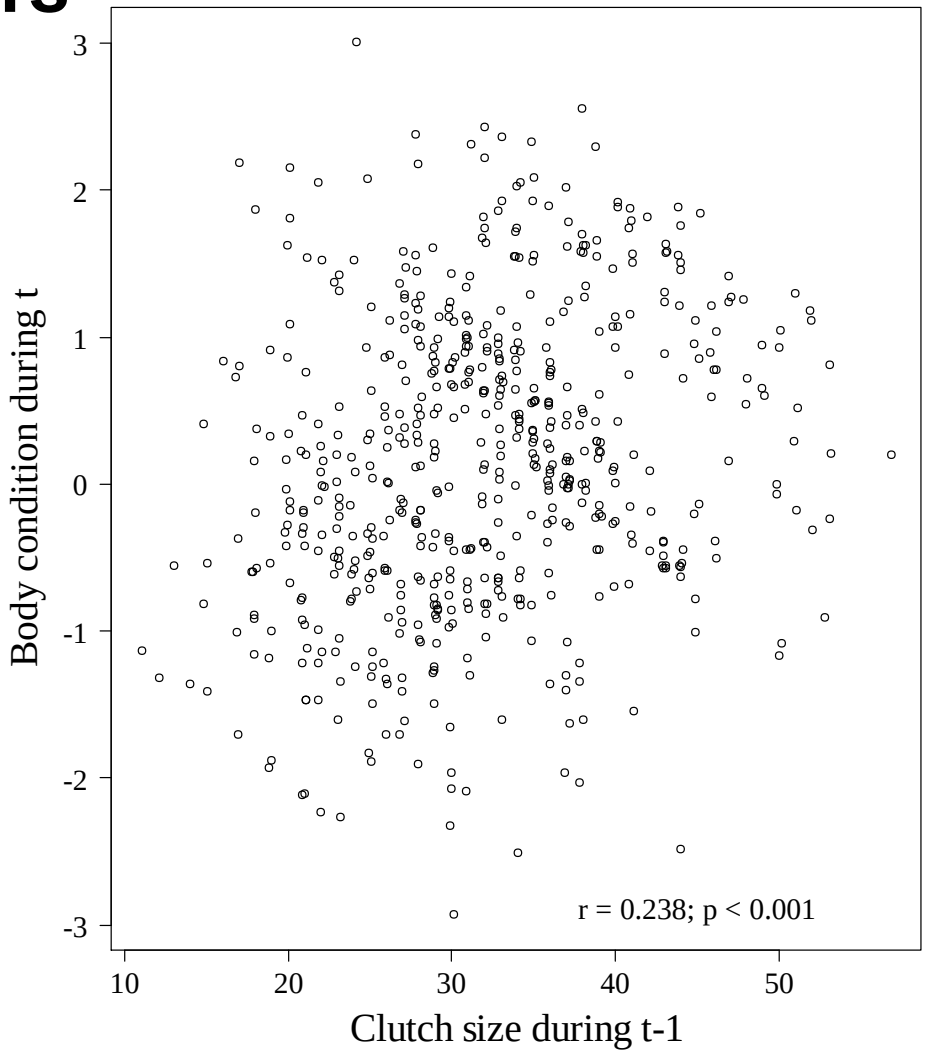

# A real-life example: ‘Wisdom’ the Laysan albatross

- First marked as an adult in 1956 (74+ years old)
- Oldest known living wild bird
- Breeds almost every year (50-60 eggs, 30+ fledglings)

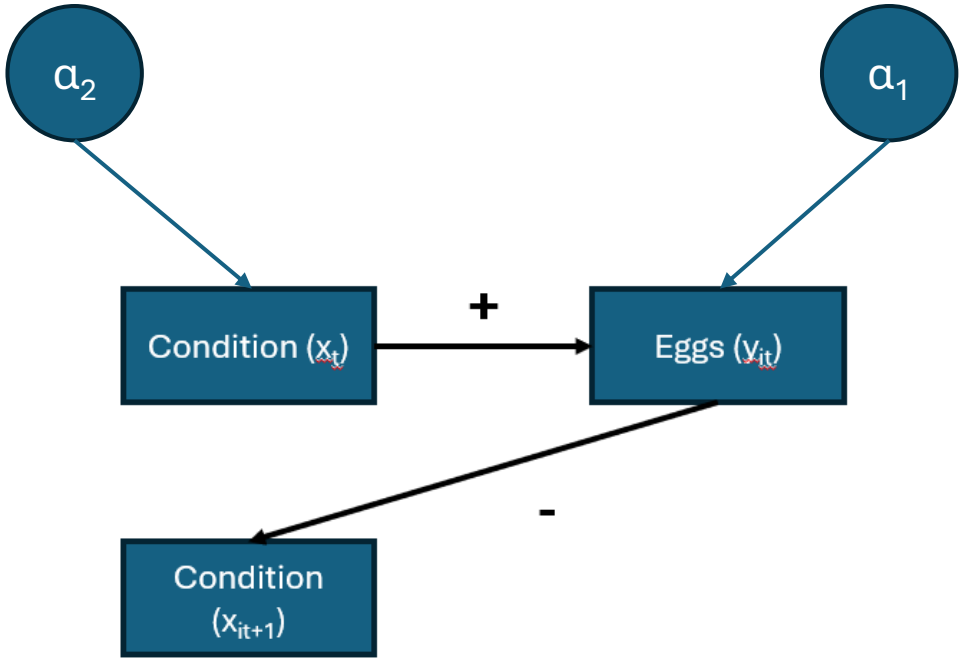


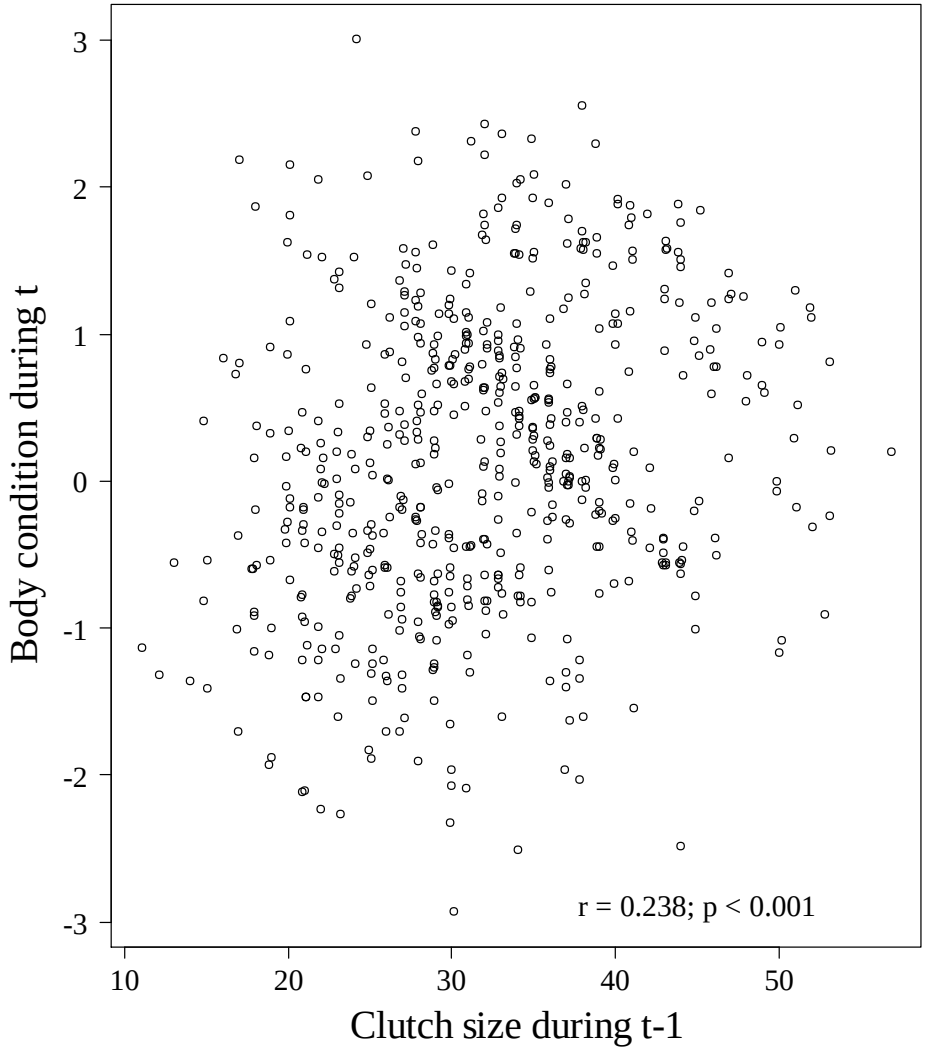
# Let's come back to simulated alligators




# We need to account for heterogeneity




**Seeing how analyses break helps us understand how they work**

## Take-homes

1. Cross-lags can lead to ‘wrong answers’ (e.g., alligator simulation, pintails) that defy theory.

## Take-homes

1. Cross-lags can lead to ‘wrong answers’ (e.g., alligators, pintails) that defy theory

2. Accounting for individual variation is crucial when attempting to estimate ‘trade-offs’ or other similar processes

## Take-homes

1. Cross-lags can lead to ‘wrong answers’ (e.g., alligators, pintails) that defy theory

2. Accounting for individual variation is crucial when attempting to estimate ‘trade-offs’ or other similar processes

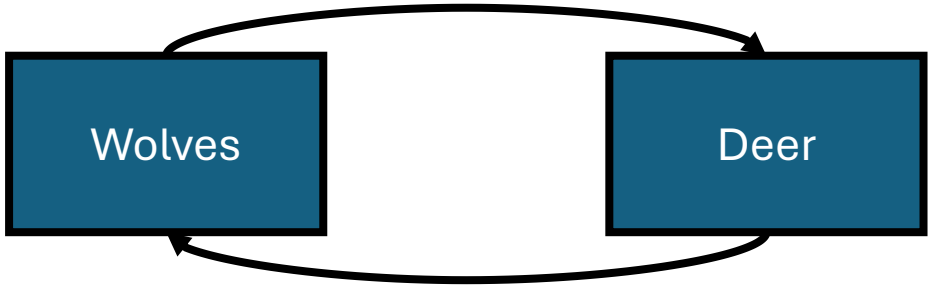
3. We can think ‘causally’ about the temporal structure of effects to clarify seemingly directed cycles

# Take-homes

1. Cross-lags can lead to ‘wrong answers’ (e.g., alligators, pintails) that defy theory

2. Accounting for individual variation is crucial when attempting to estimate ‘trade-offs’ or other similar processes

3. We can think ‘causally’ about the temporal structure of effects to clarify seemingly directed cycles

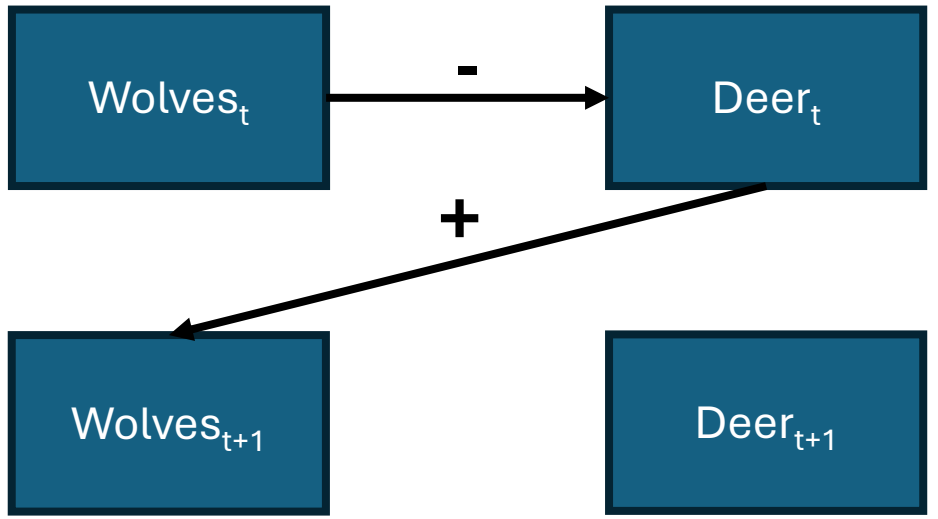


# Take-homes

3. We can think ‘causally’ about the temporal structure of effects to clarify seemingly directed cycles

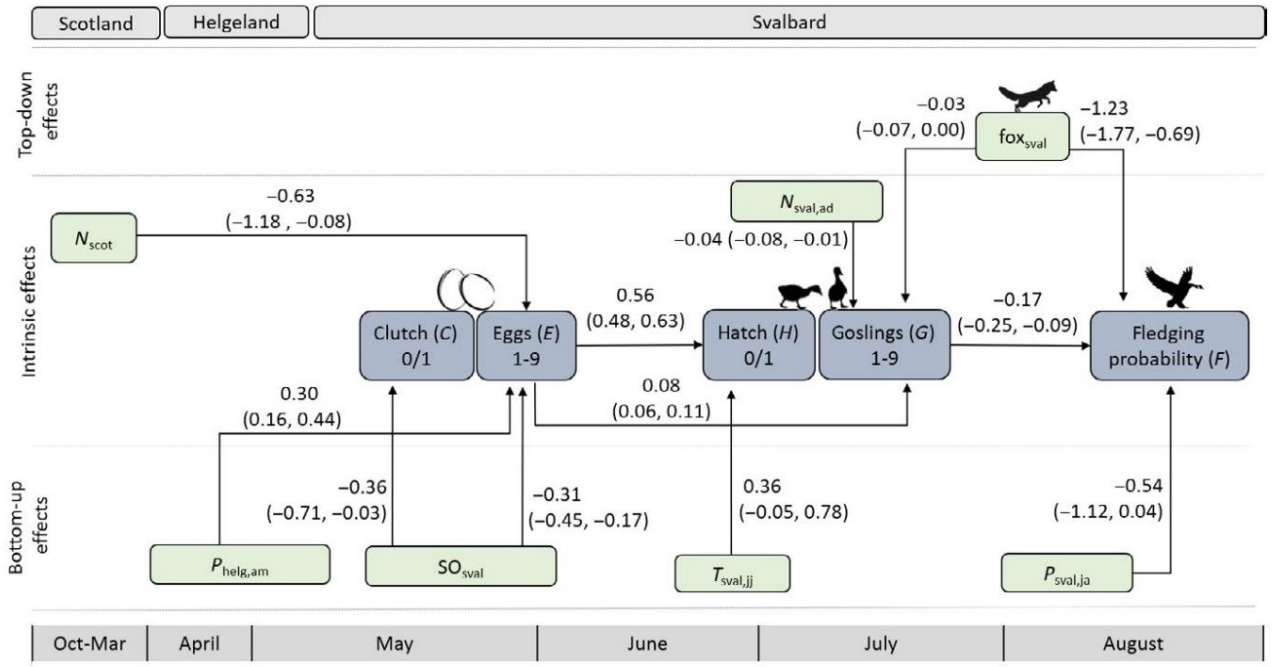
$$\frac{\delta d}{\delta t} = f(w)$$

$$\frac{\delta w}{\delta t} = f(d)$$



# Take-homes

4. We don’t have to use ‘cross-lags’ across years, simply modeling sequential processes within a season can be extremely valuable




Layton-Matthews et al. **(2019)** *Global Change Biology*