

Specialization trumps competition:

Counter-intuitive effects of intraspecific competition on population niche width

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on the Menu:

Effect of population density on niche use

- 1) Explicit experimental test
- 2) Simple model of optimal resource use
- 3) Full parameterization of the model, prediction & test
- 4) Test of assumptions and modifications to initial model

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Effect of population density on niche use

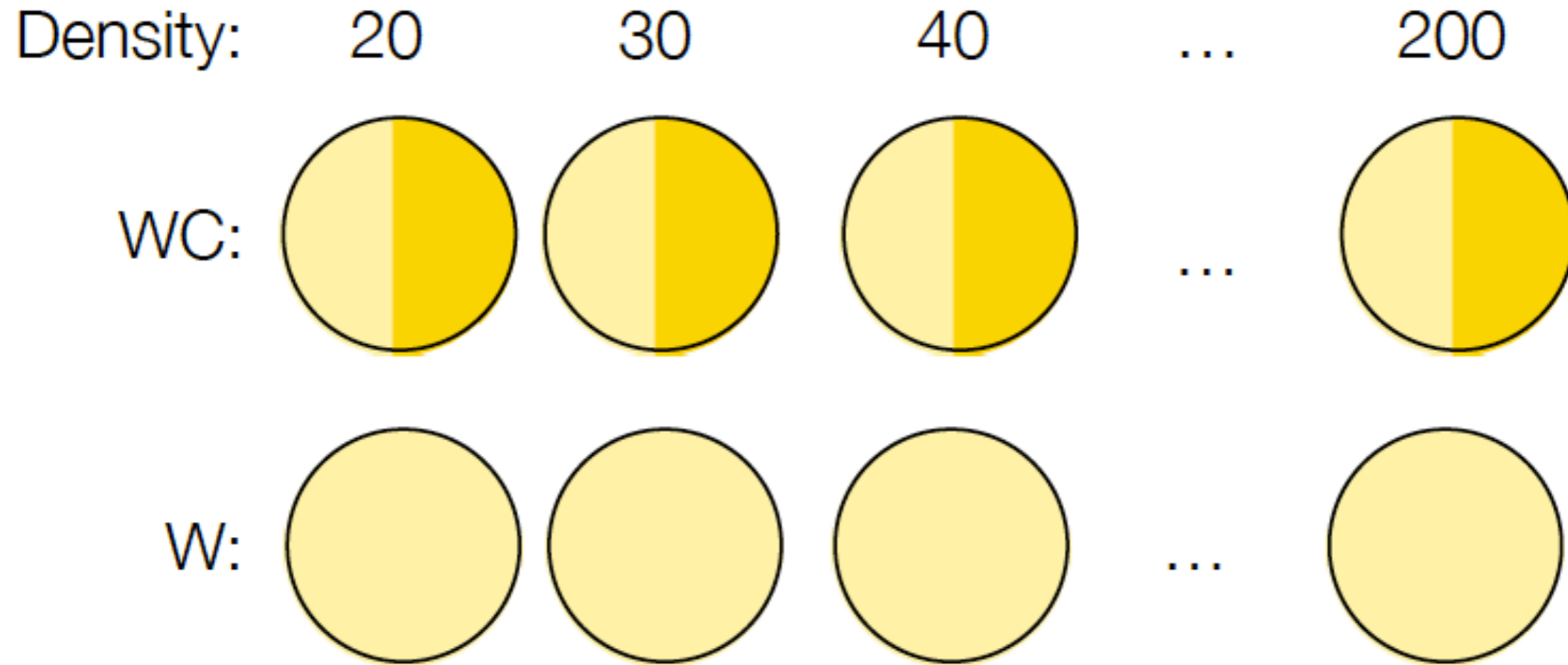
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Tribolium castaneum beetles

- short generation time (~4 weeks), and easily maintained in great numbers in the lab, ancestral resource is wheat
- competition at the larval and adult stages
- stable isotopes can be used to quantify proportion of resource used when offered wheat (ancestral resource) and corn (suboptimal, novel resource)



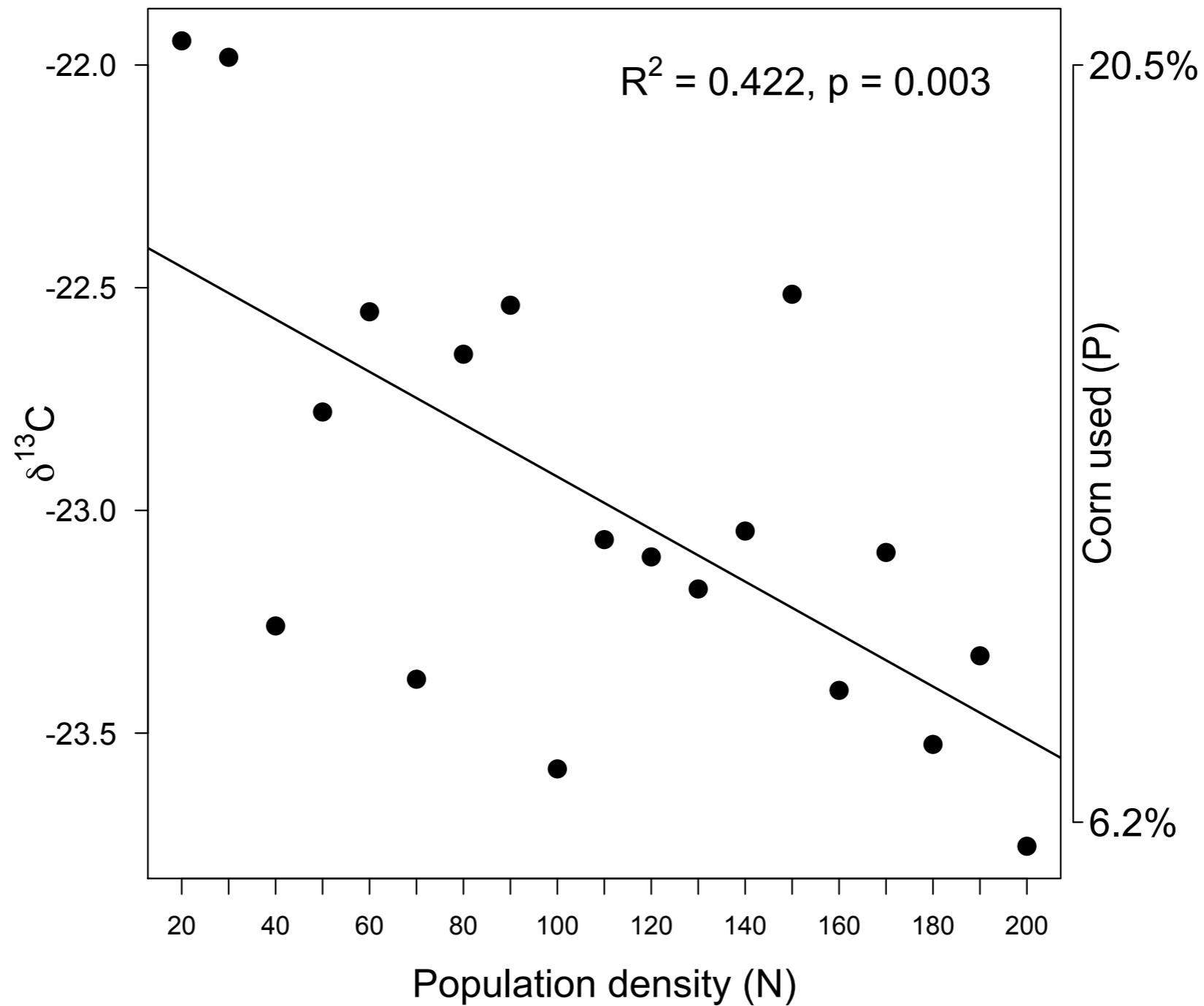
Experimental design



- manipulate population density over a 10-fold range
- wait 2 weeks
- estimate fitness (per capita productivity)
- estimate niche width in adults (using isotopes), and larvae (resource preference assays)

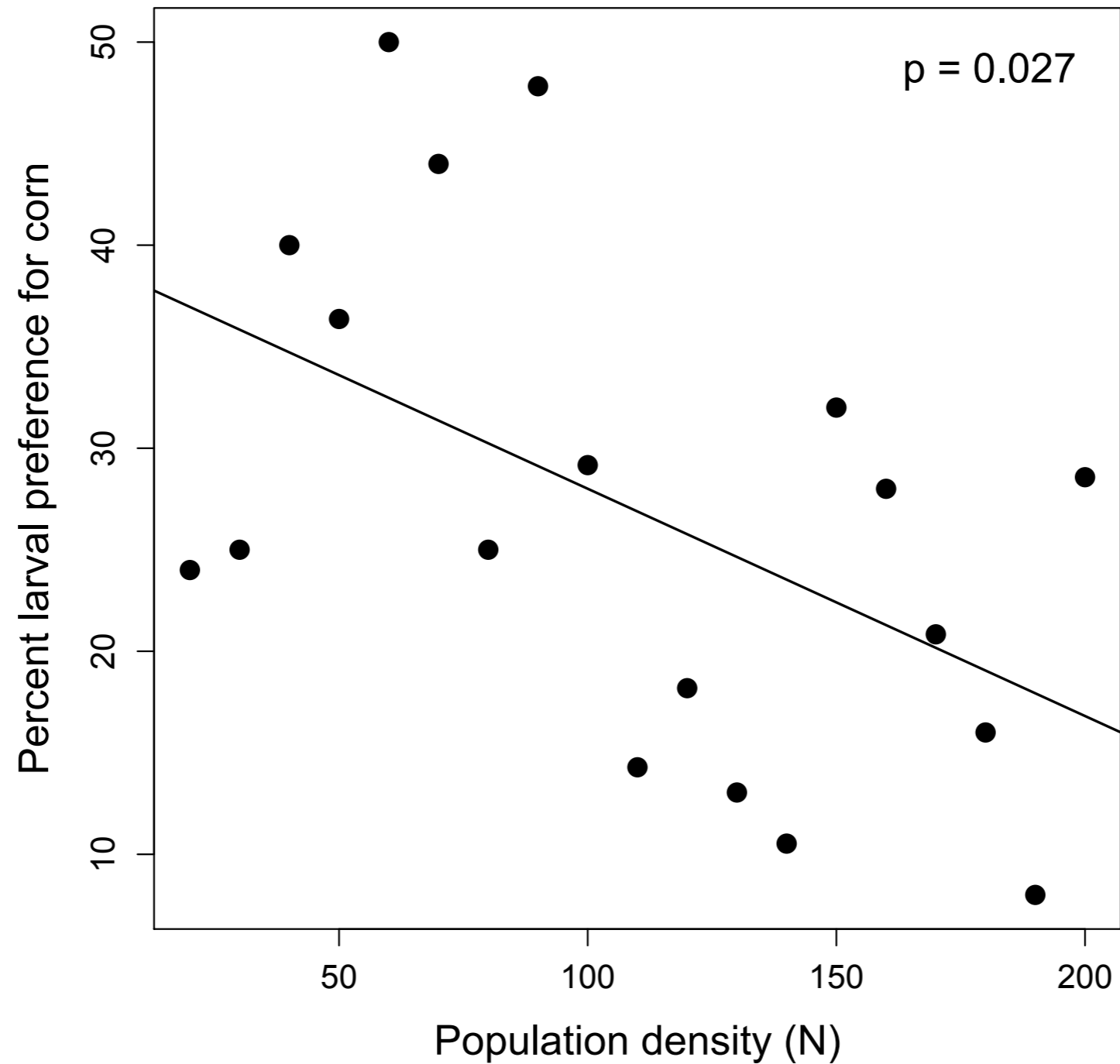
Increased population density leads to niche compression

Proportion of novel resource used by adults



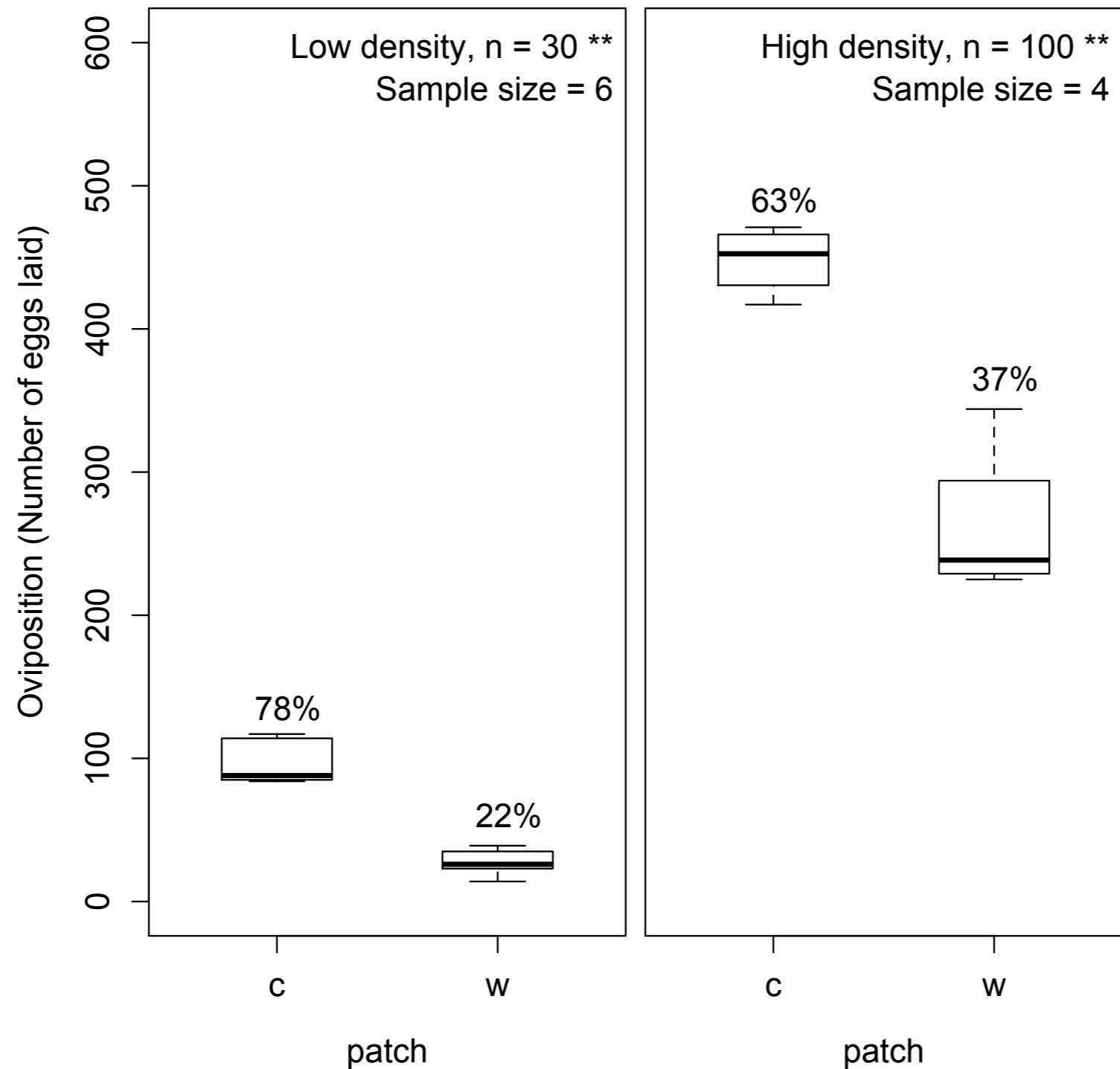
Increased population density leads to niche compression

Proportion of novel resource preferred by larvae



Increased population density leads to niche compression

Oviposition in novel vs ancestral resource at low vs high density

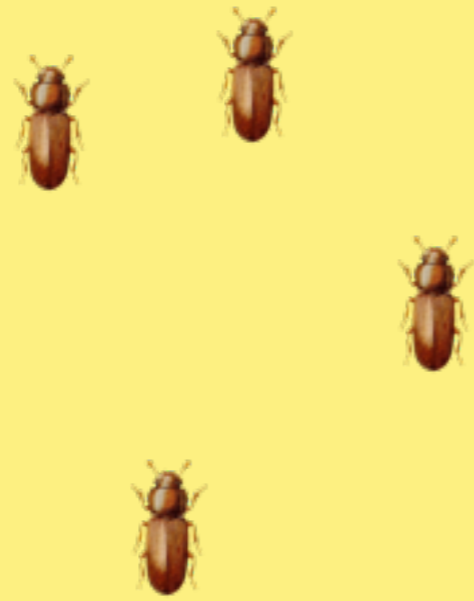


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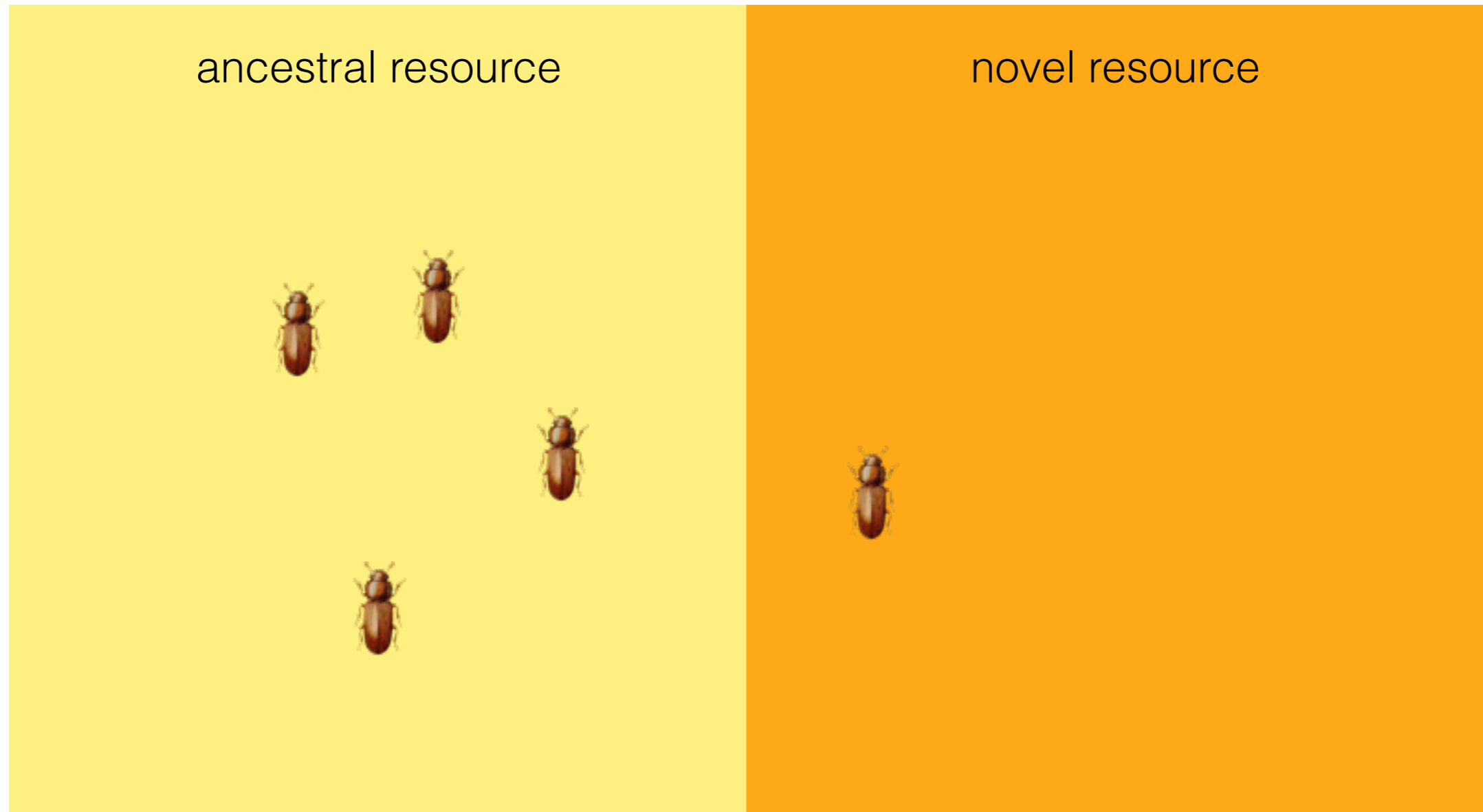
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ancestral resource



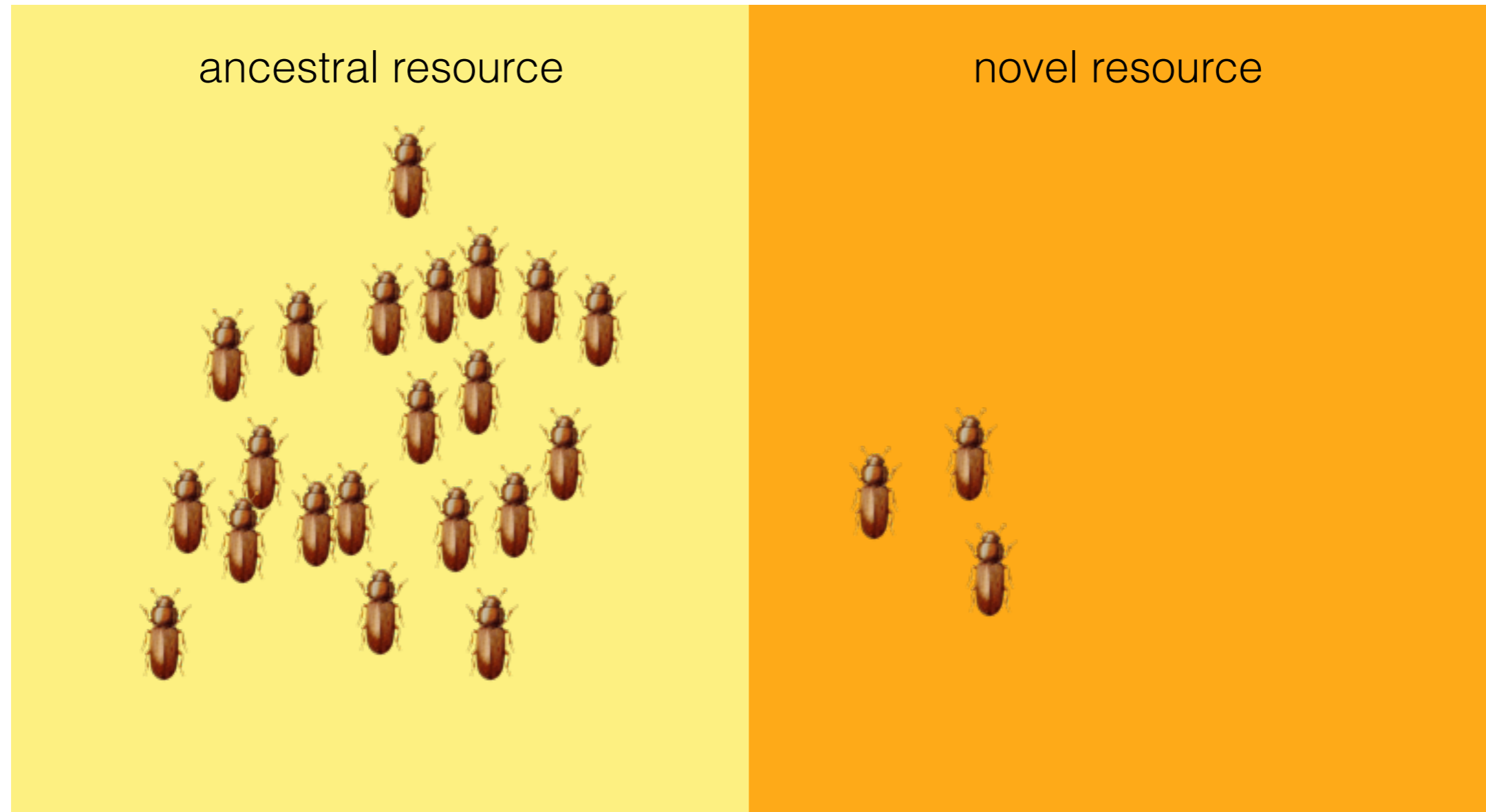
novel resource



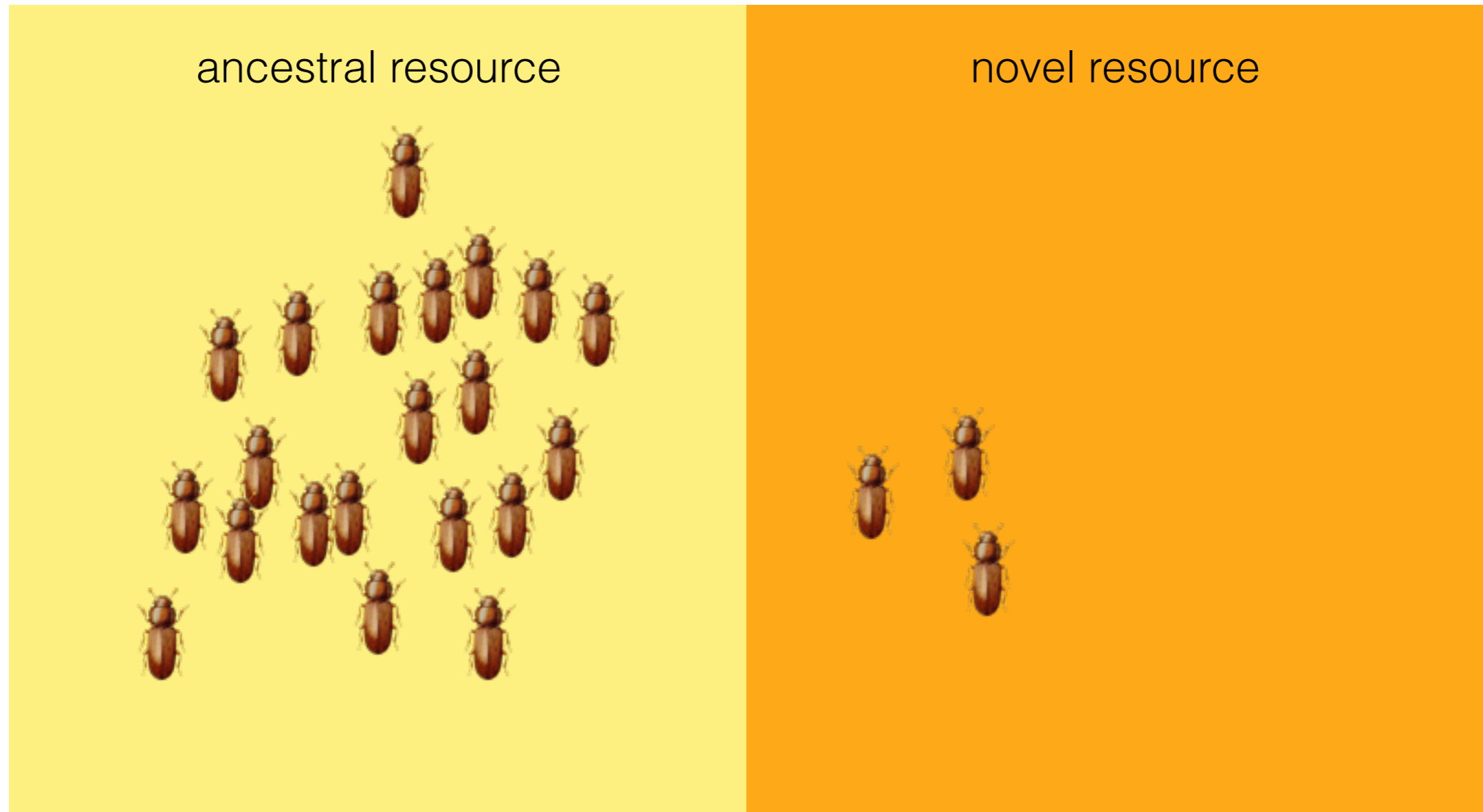


Population mean fitness $w = r_a(1-P) + r_n(P)$

r_i = per capita productivity on resource i
 P = proportional use of the novel resource



Population mean fitness $w = r_a(1-P) + r_n(P)$



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Density-dependent productivity: $r_a = r'_a(1 - \alpha_a N(1-P))$

$r_n = r'_n(1 - \alpha_n N(P))$

r'_i = density independent productivity on resource i (when $N = 1$)

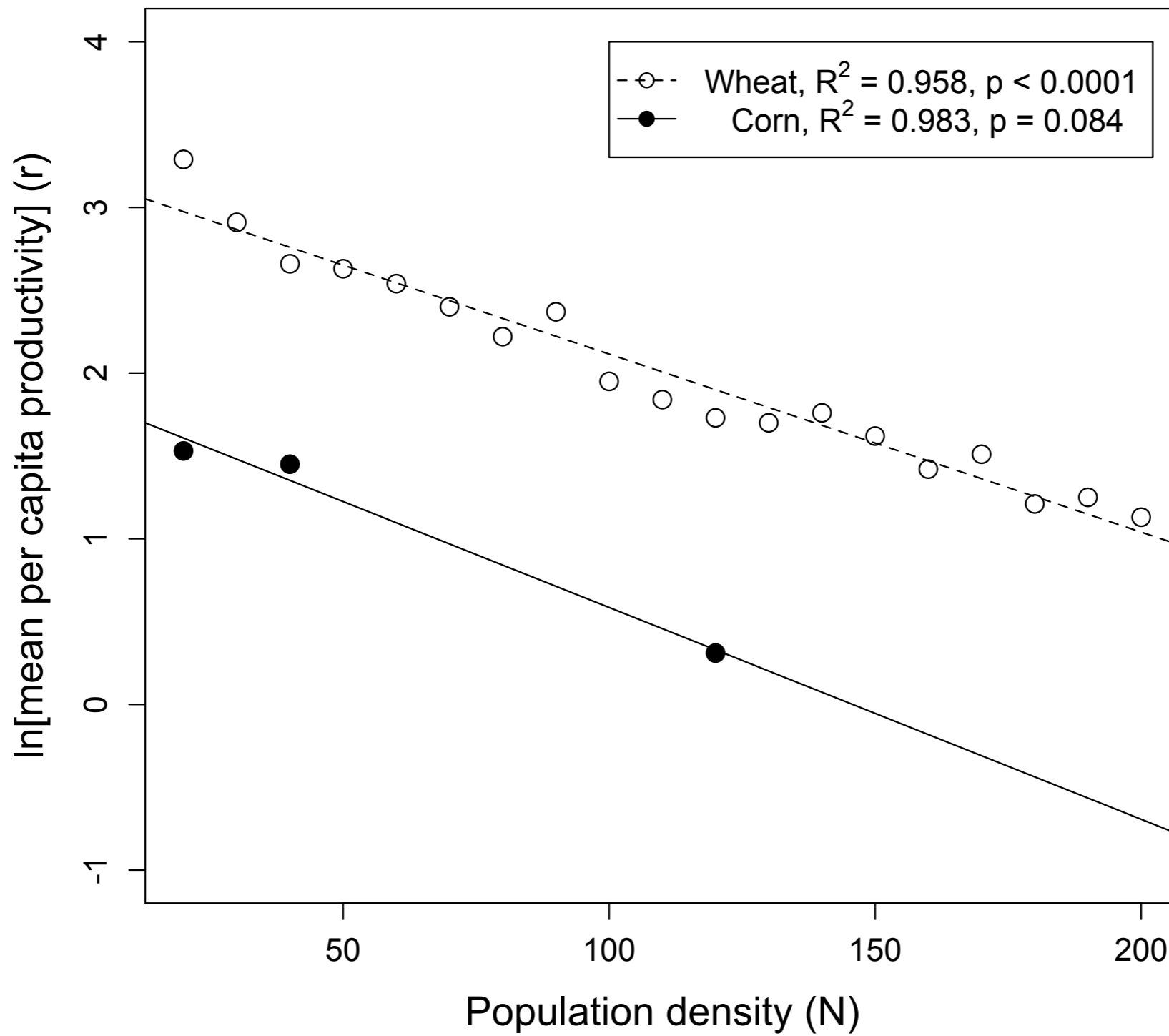
α_i = intraspecific competition coefficient for resource i

N = population density

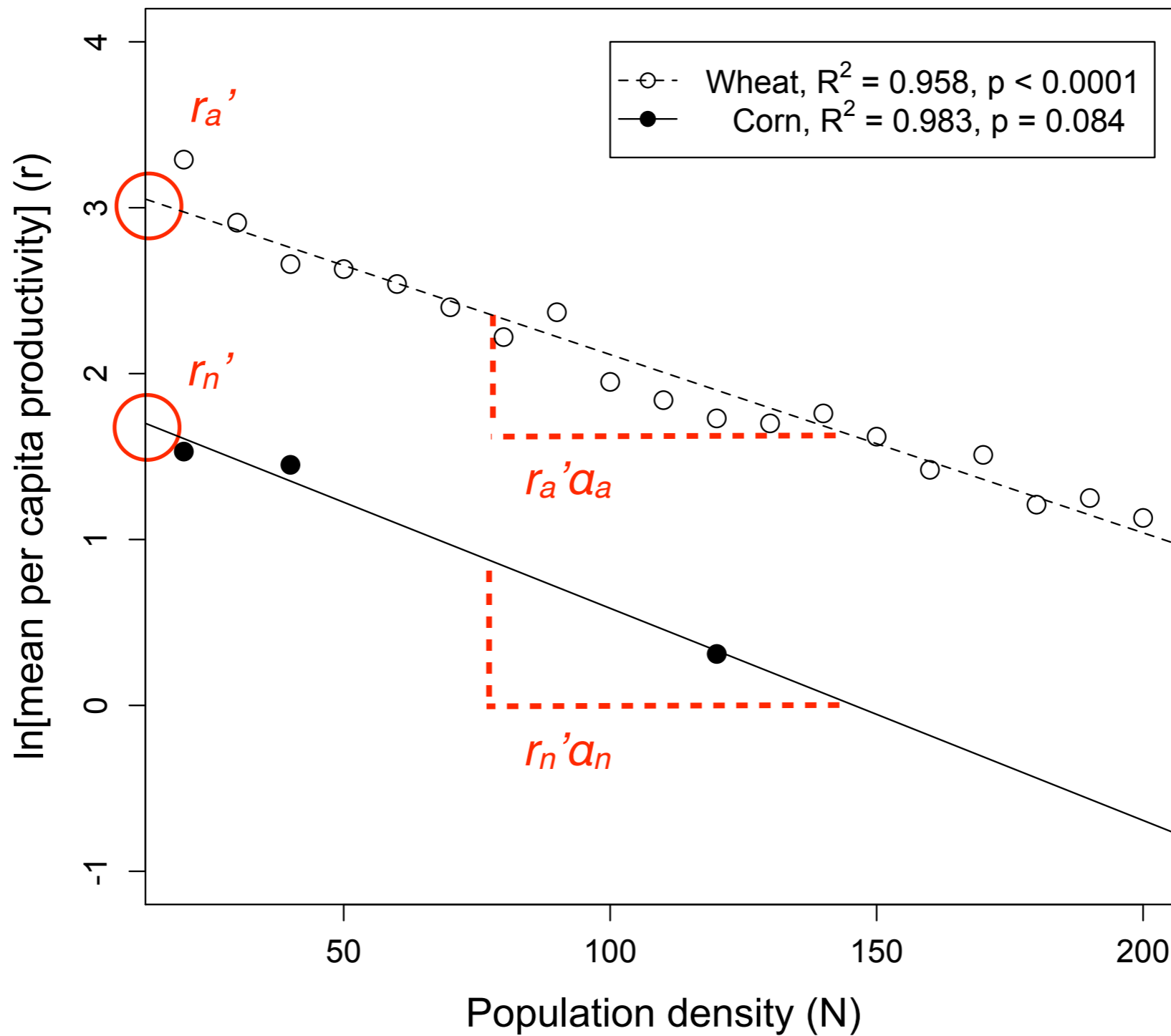
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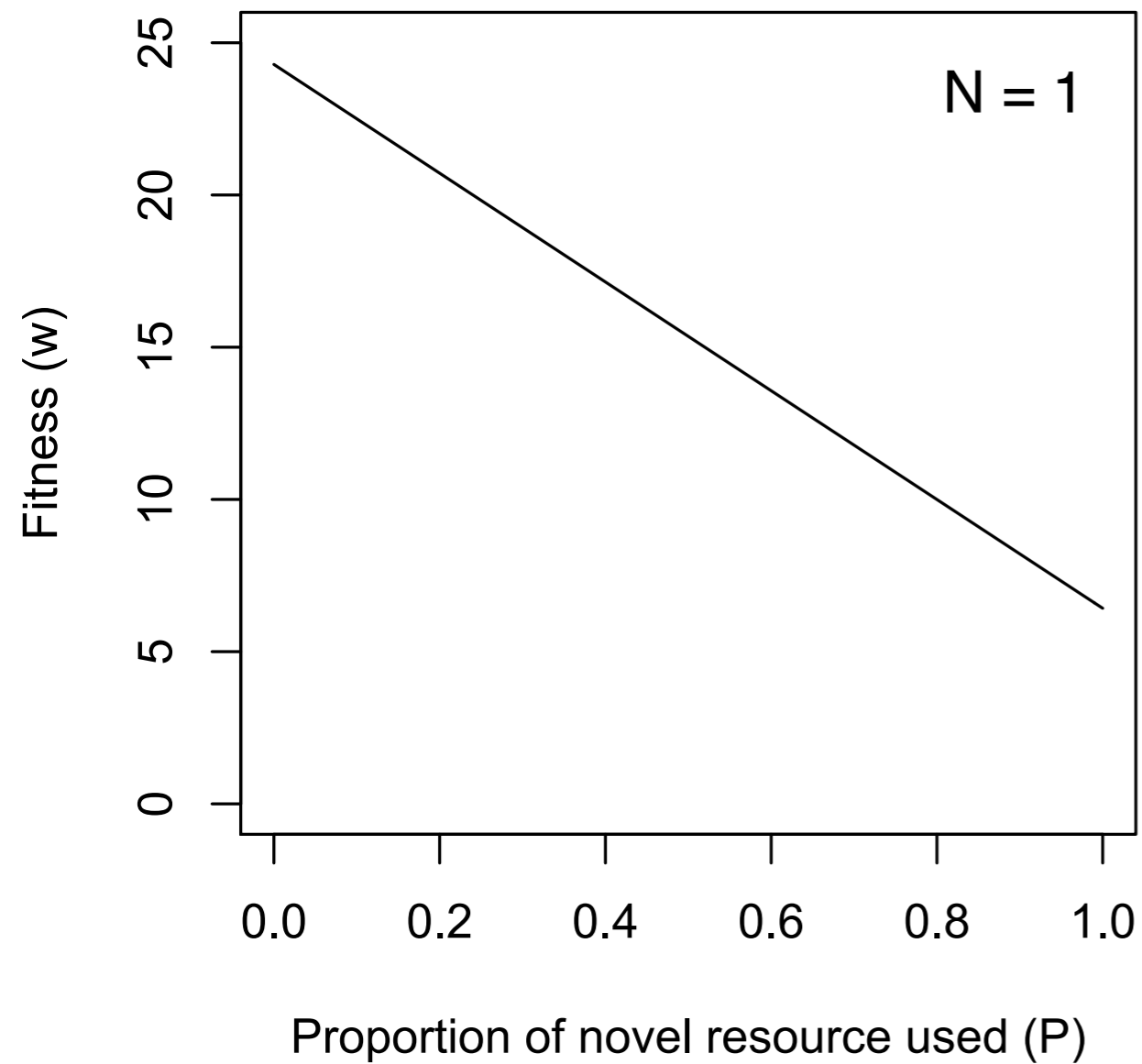
$$w = (1 - P)e^{[ra'(1 + \alpha a(N - 1)(1 - P))]} + Pe^{[rn'(1 + an(N - 1)(P))]}$$



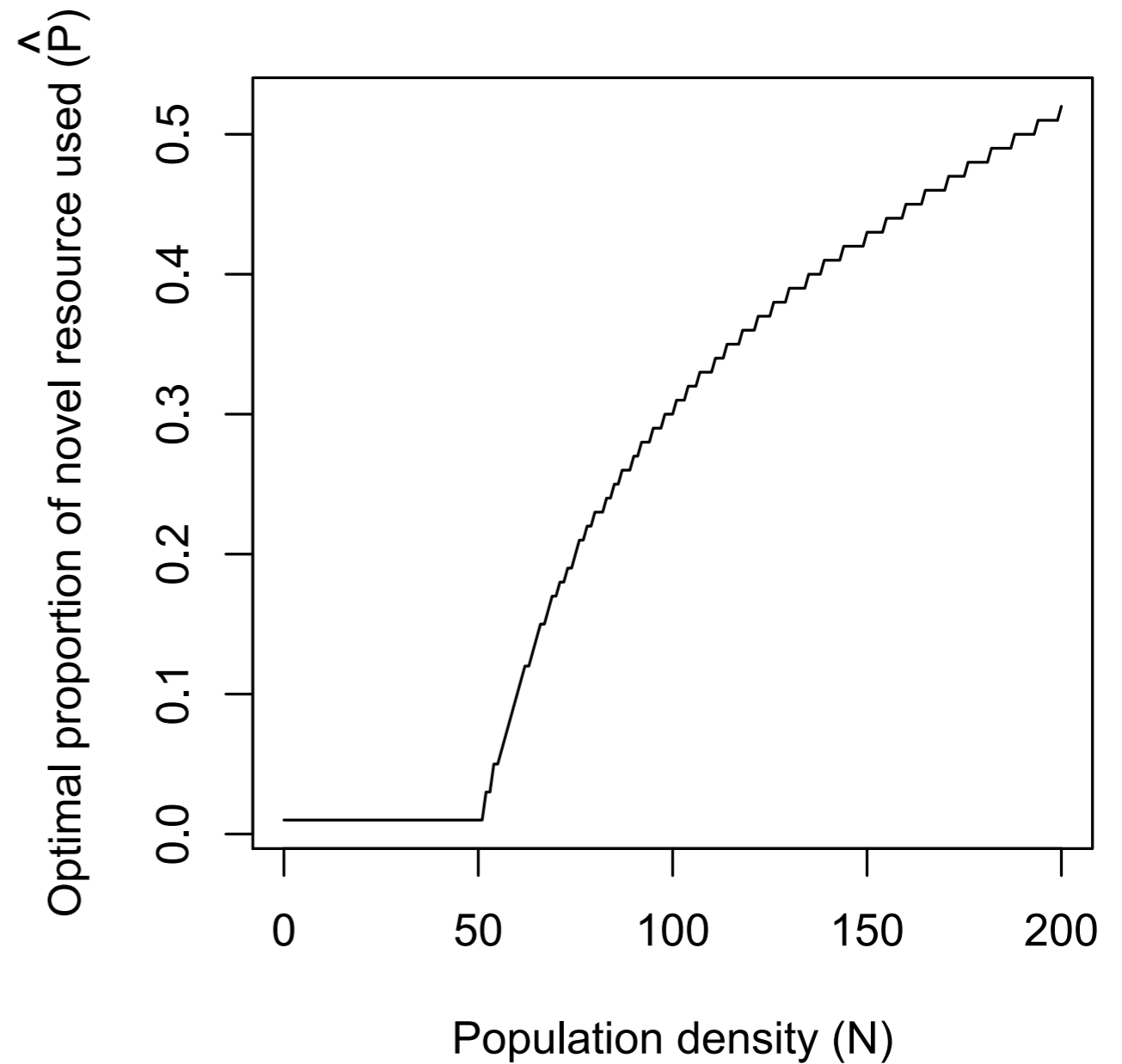
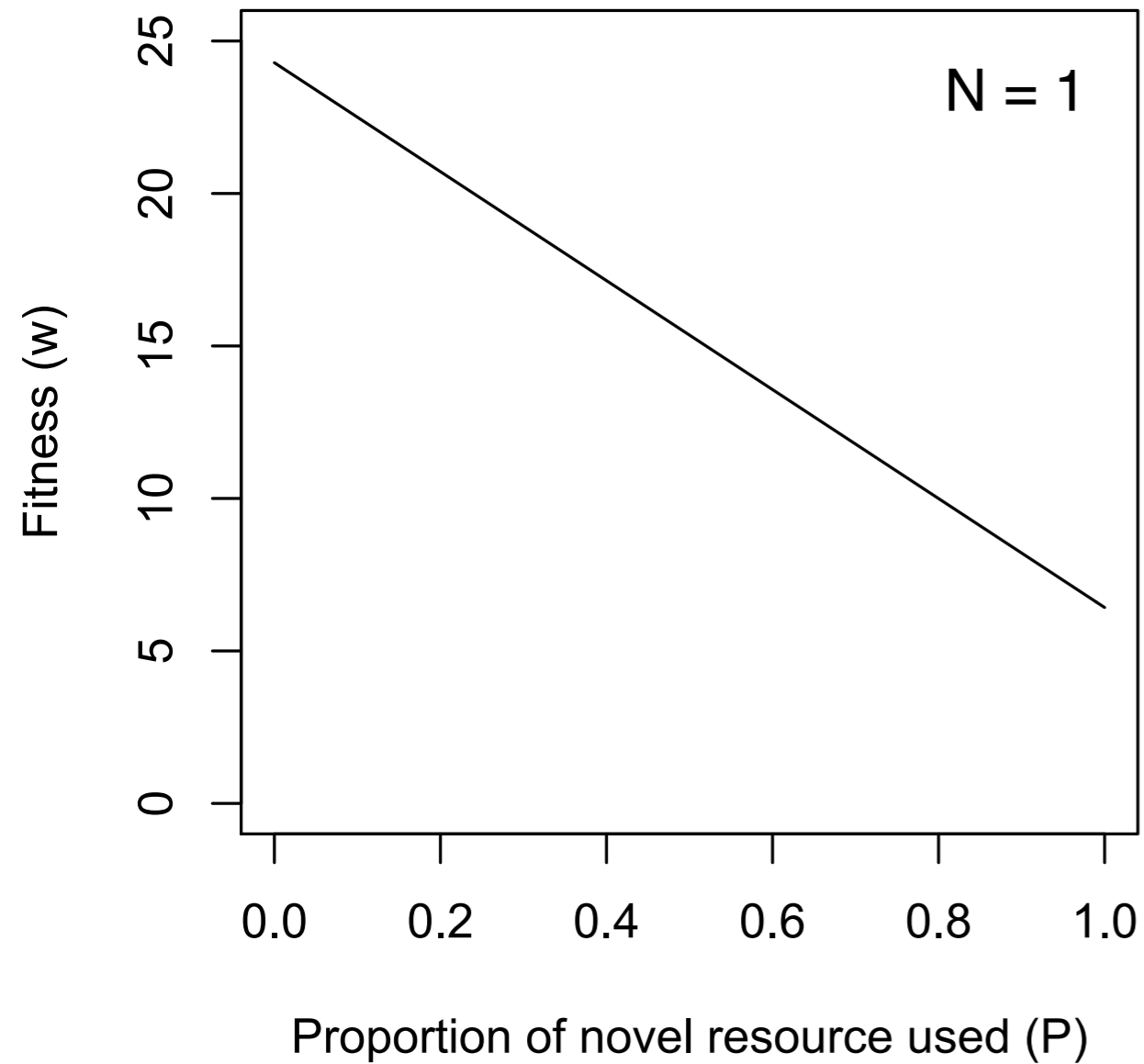
$$w = (1 - P)e^{[ra'(1 + \alpha_a(N - 1)(1 - P))]} + Pe^{[rn'(1 + \alpha_n(N - 1)(P))]}$$

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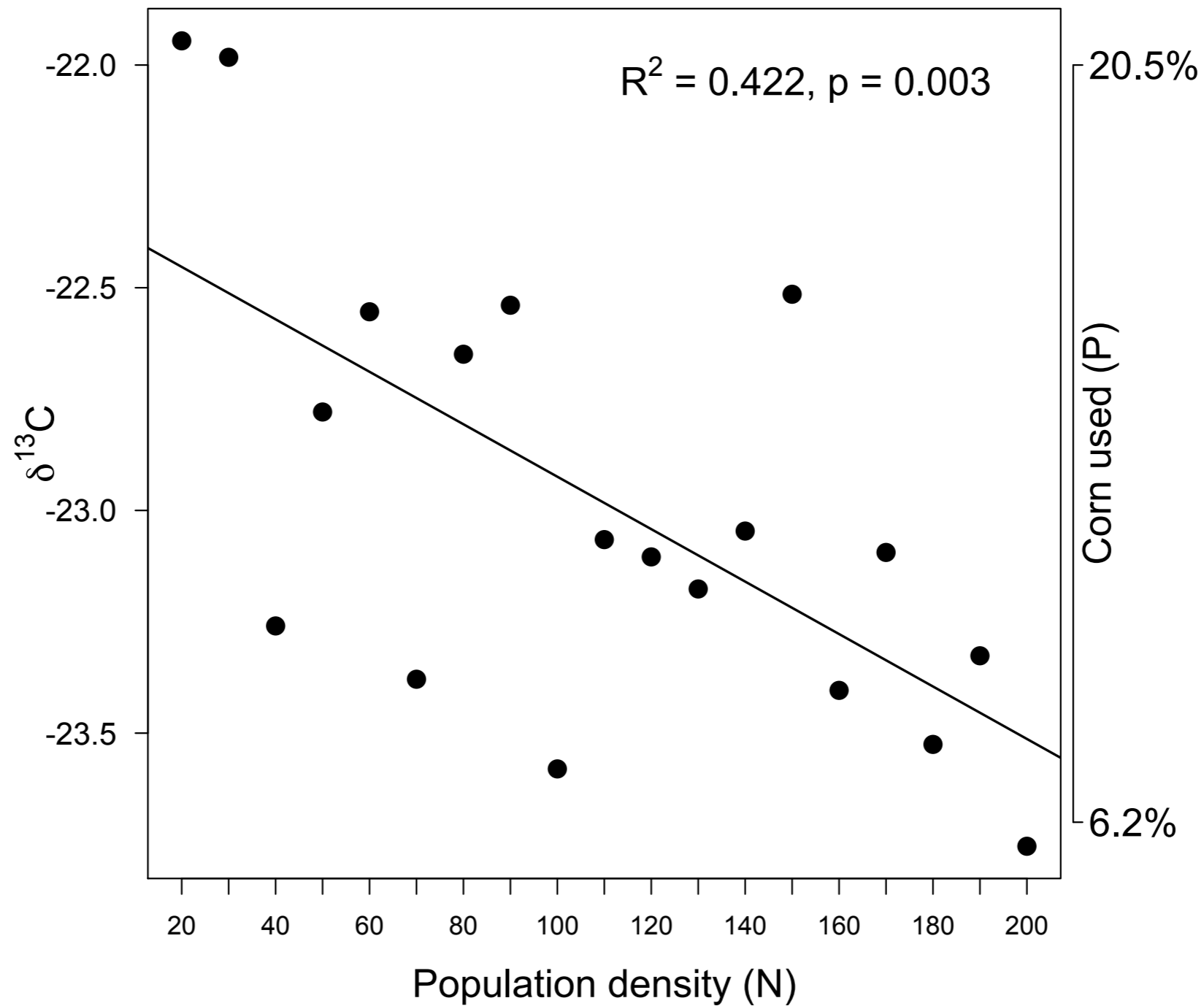


$$w = (1 - P)e^{[ra'(1 + \alpha a(N - 1)(1 - P))]} + Pe^{[rn'(1 + \alpha n(N - 1)(P))]}$$



Increased population density leads to niche compression

Proportion of novel resource used by adults



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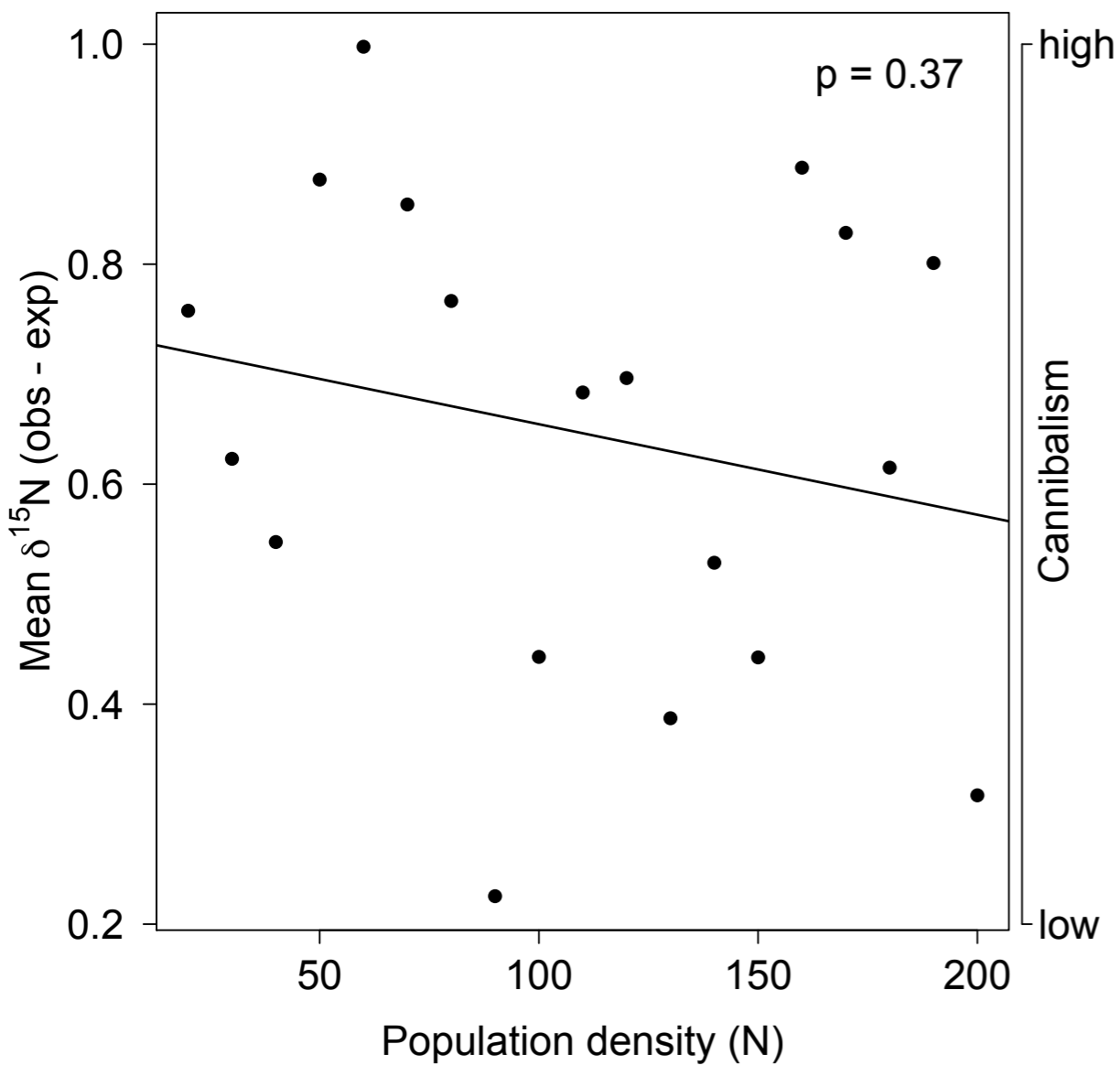
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Assumptions of the model

- i) Individuals compete over two (and only two) resources
- ii) Competition equally reduces the real and perceived value of resources
- iii) Fitness effects of using either or both resources are strictly additive
- iv) No trade-offs between using the two resources

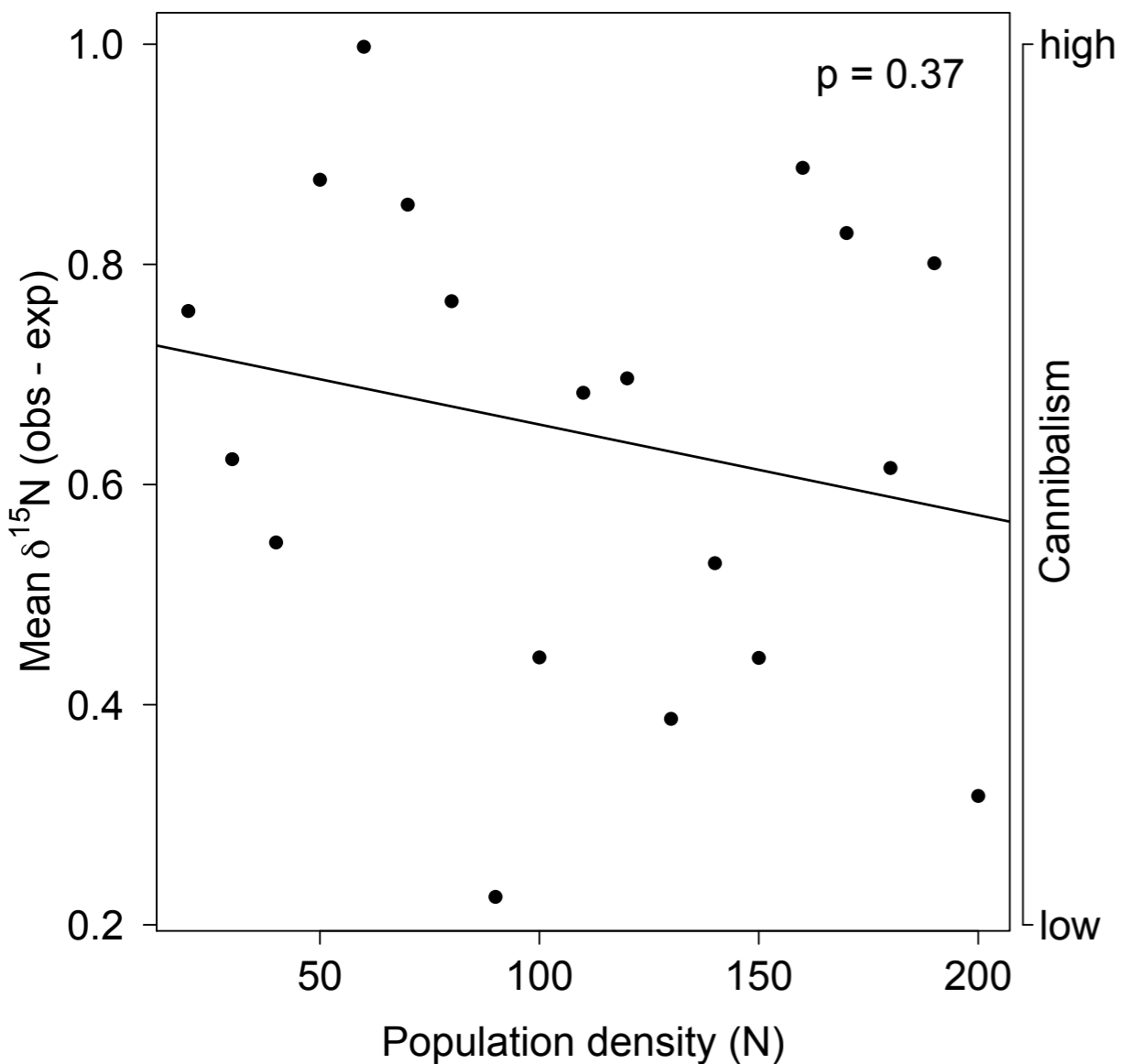
Cannibalism is not density dependent

Mean $\delta^{15}\text{N}$

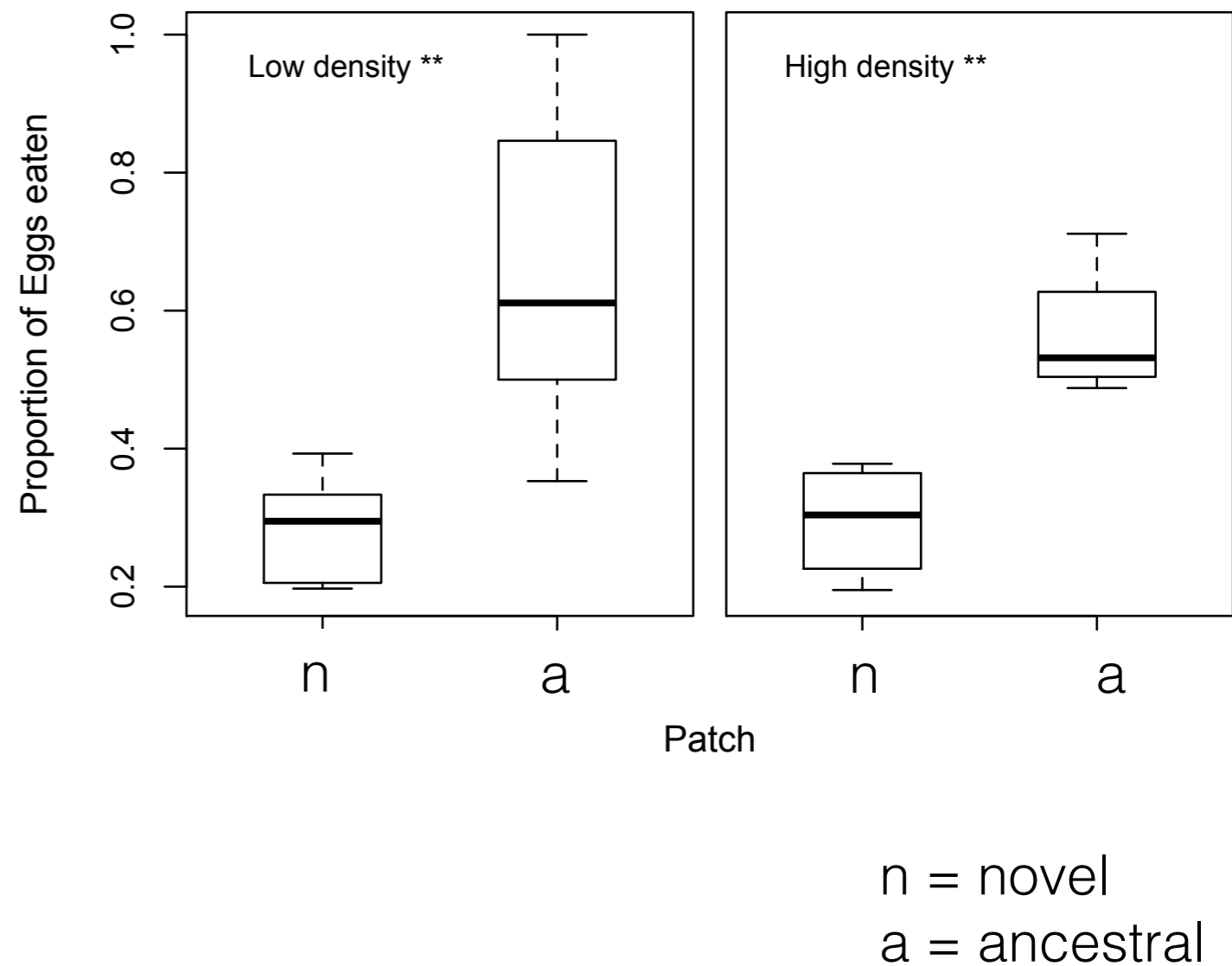


Cannibalism is not density dependent

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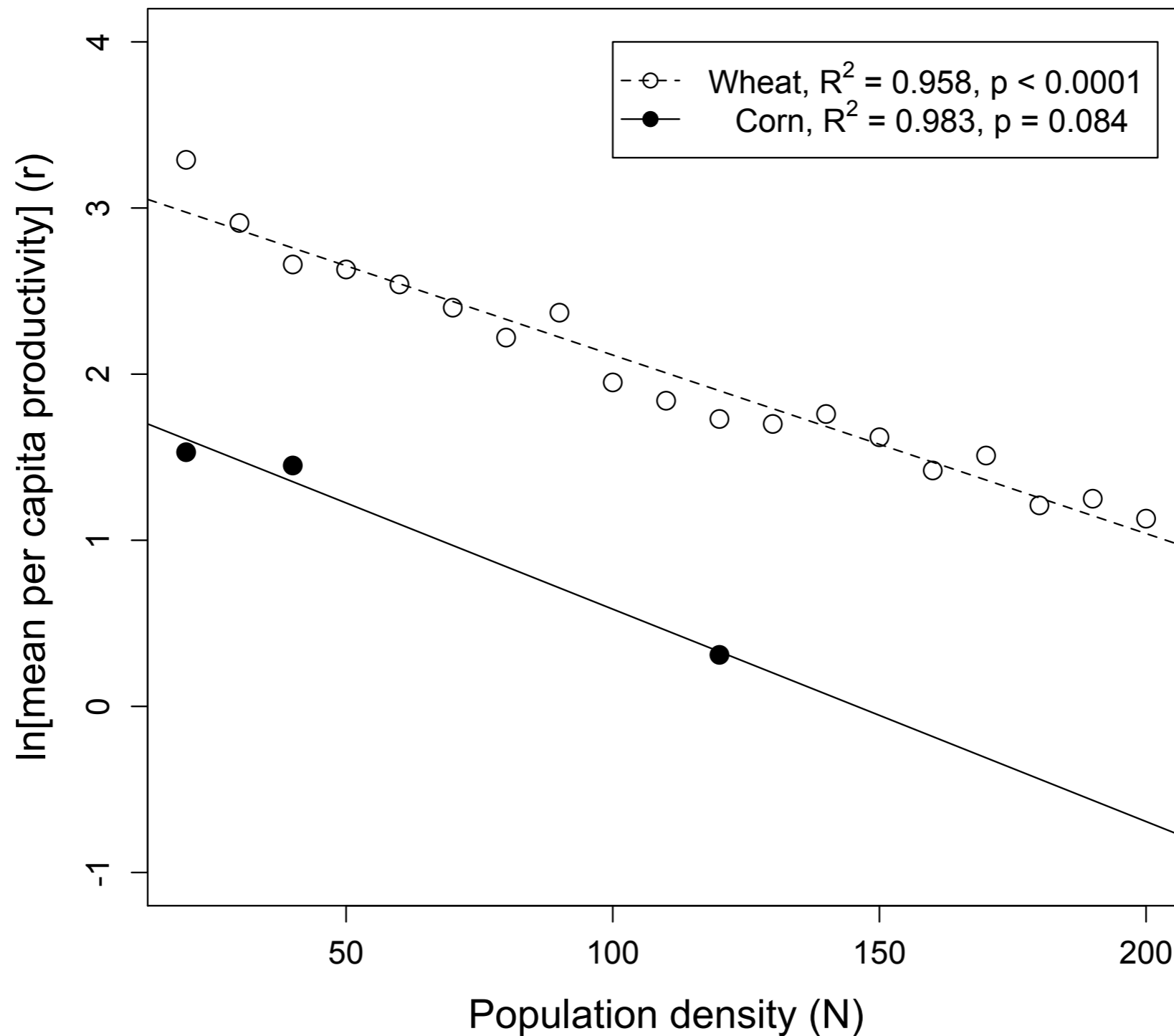
Number of eggs cannibalized



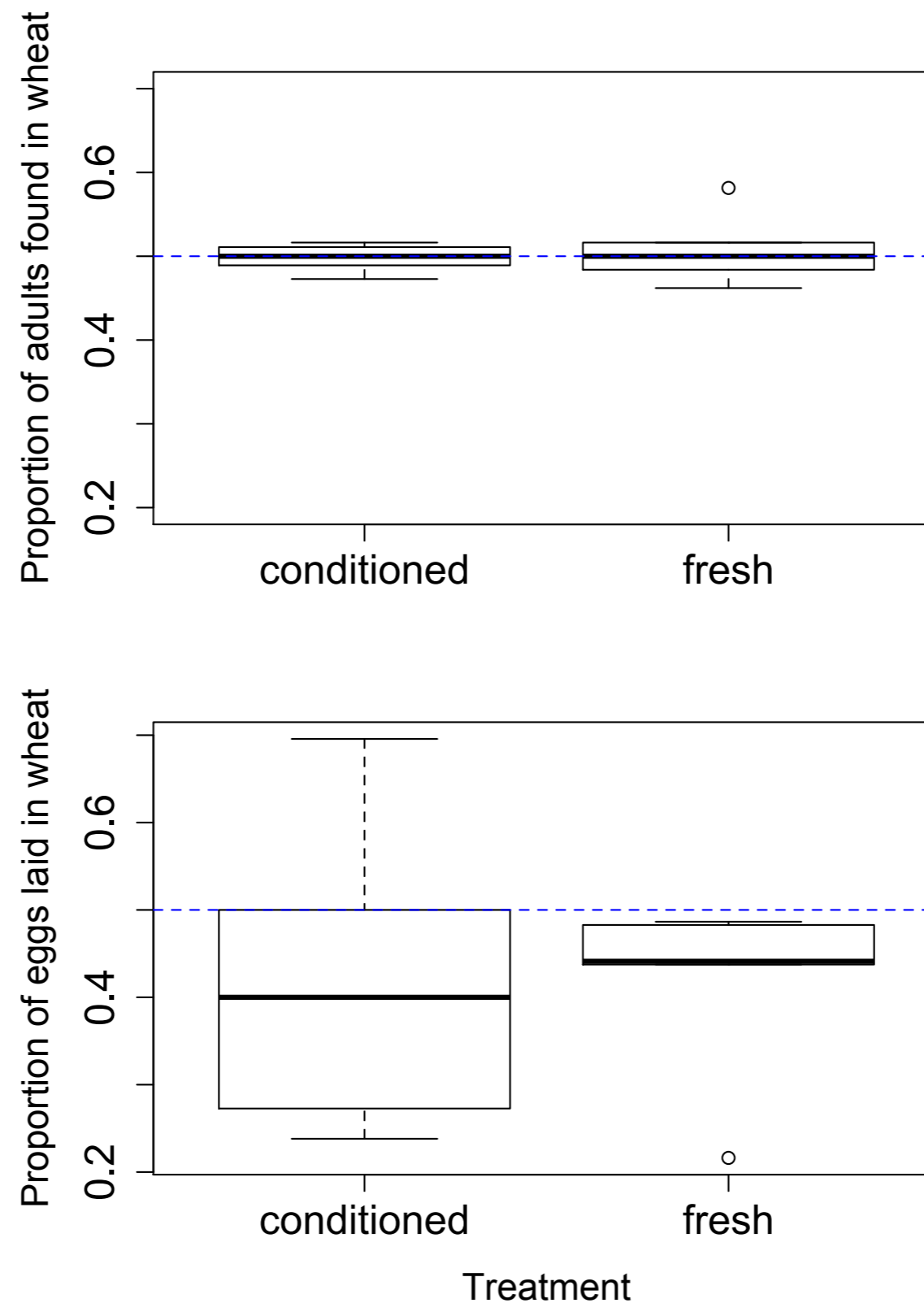
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Fitness on W or C declines at the same rate



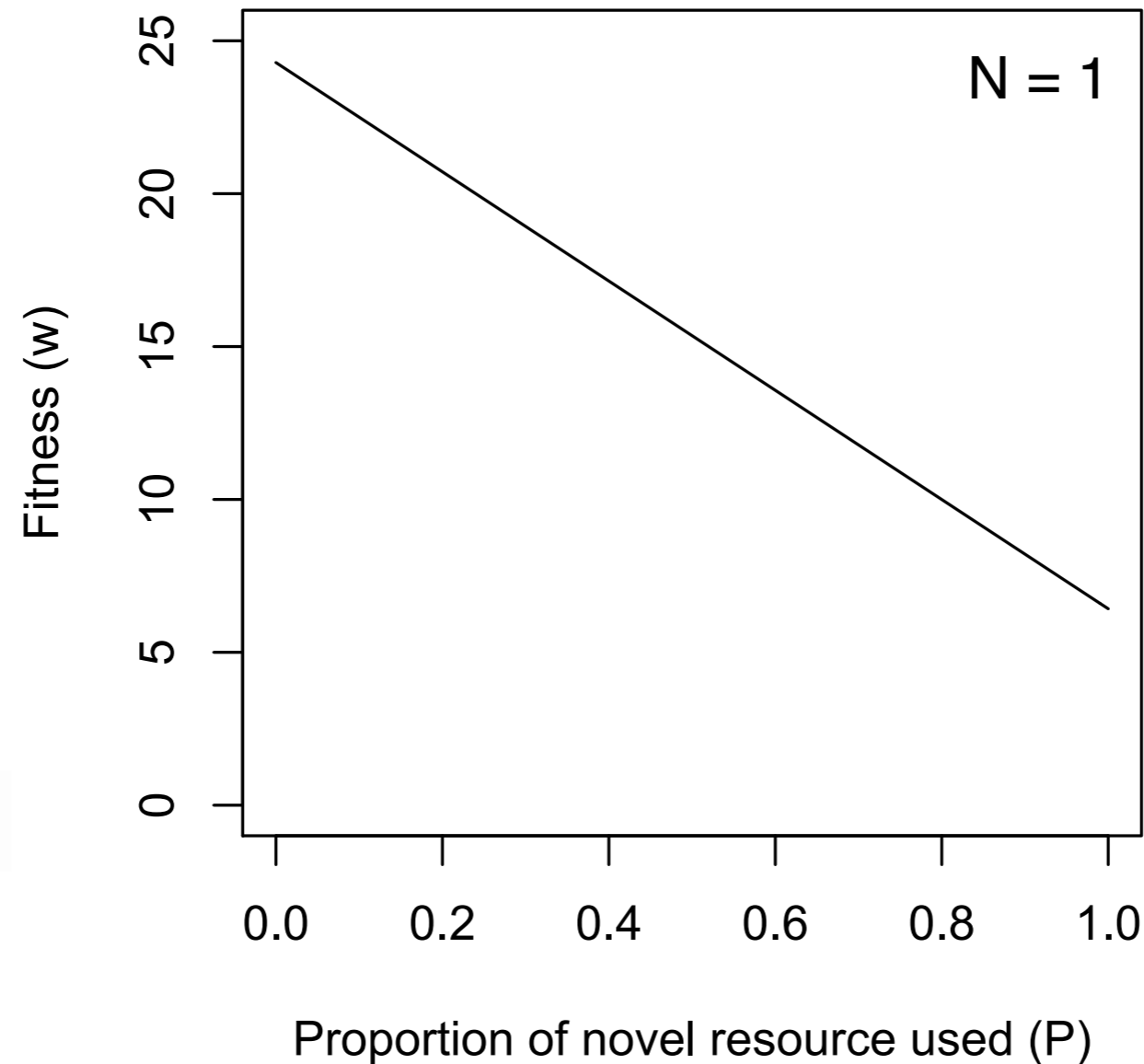
Equal perceived value at high density



Assumptions of the model

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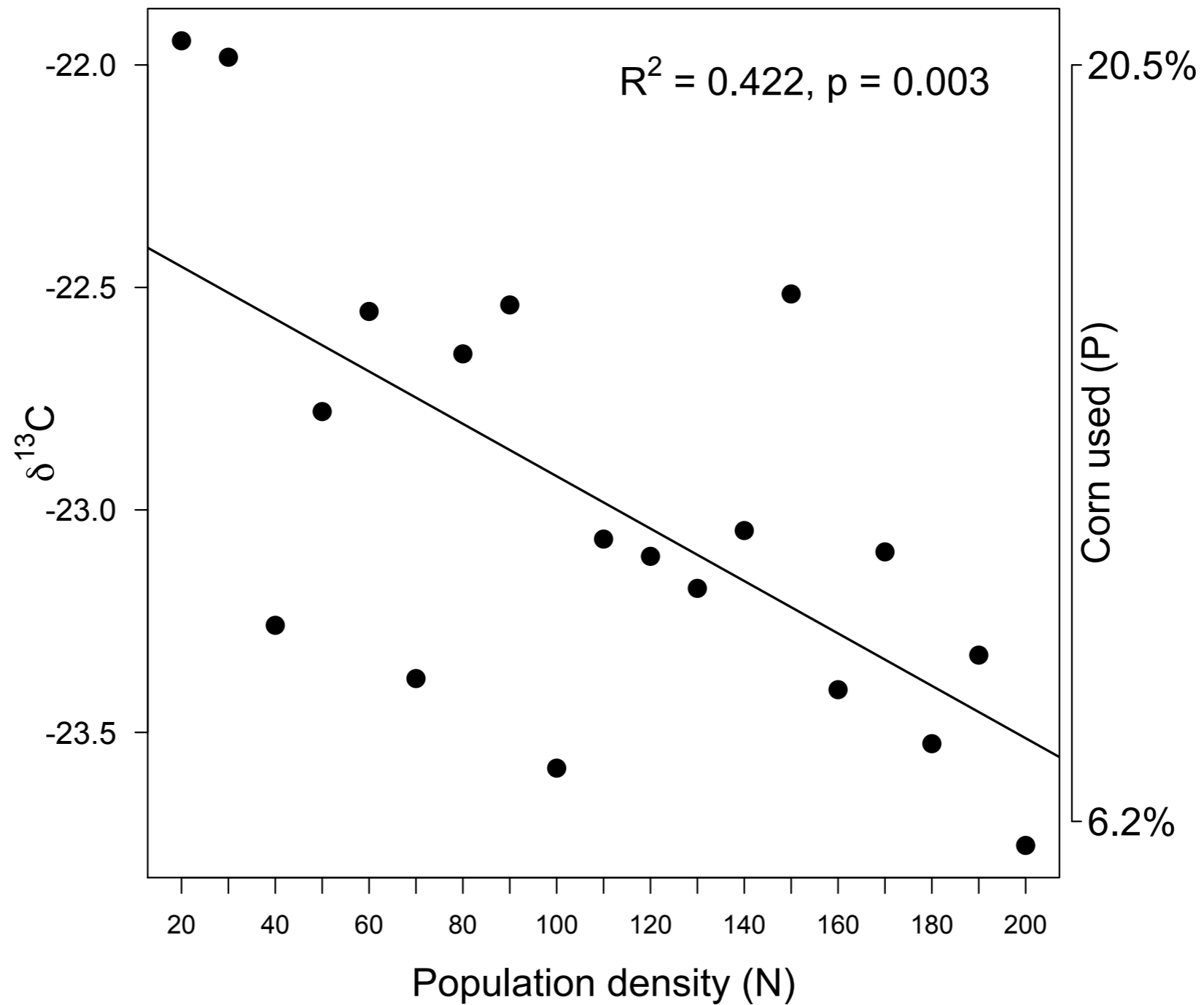
Additive effects at low density



At low density, fitness is always maximized by specializing on the more profitable ancestral resource, because $r_a > r_n$.

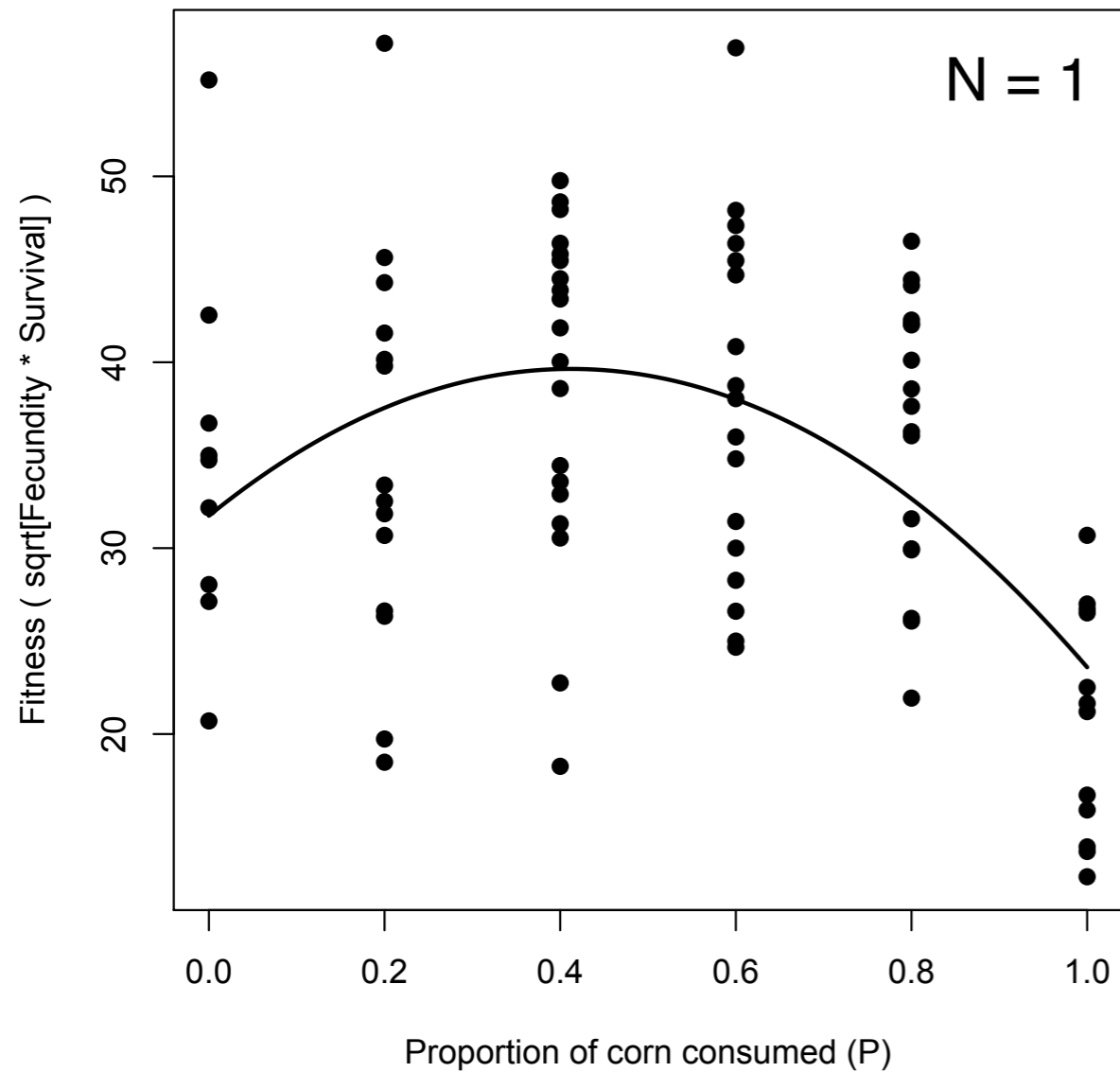
BUT,

BUT, $P \sim 0.2$ at low density



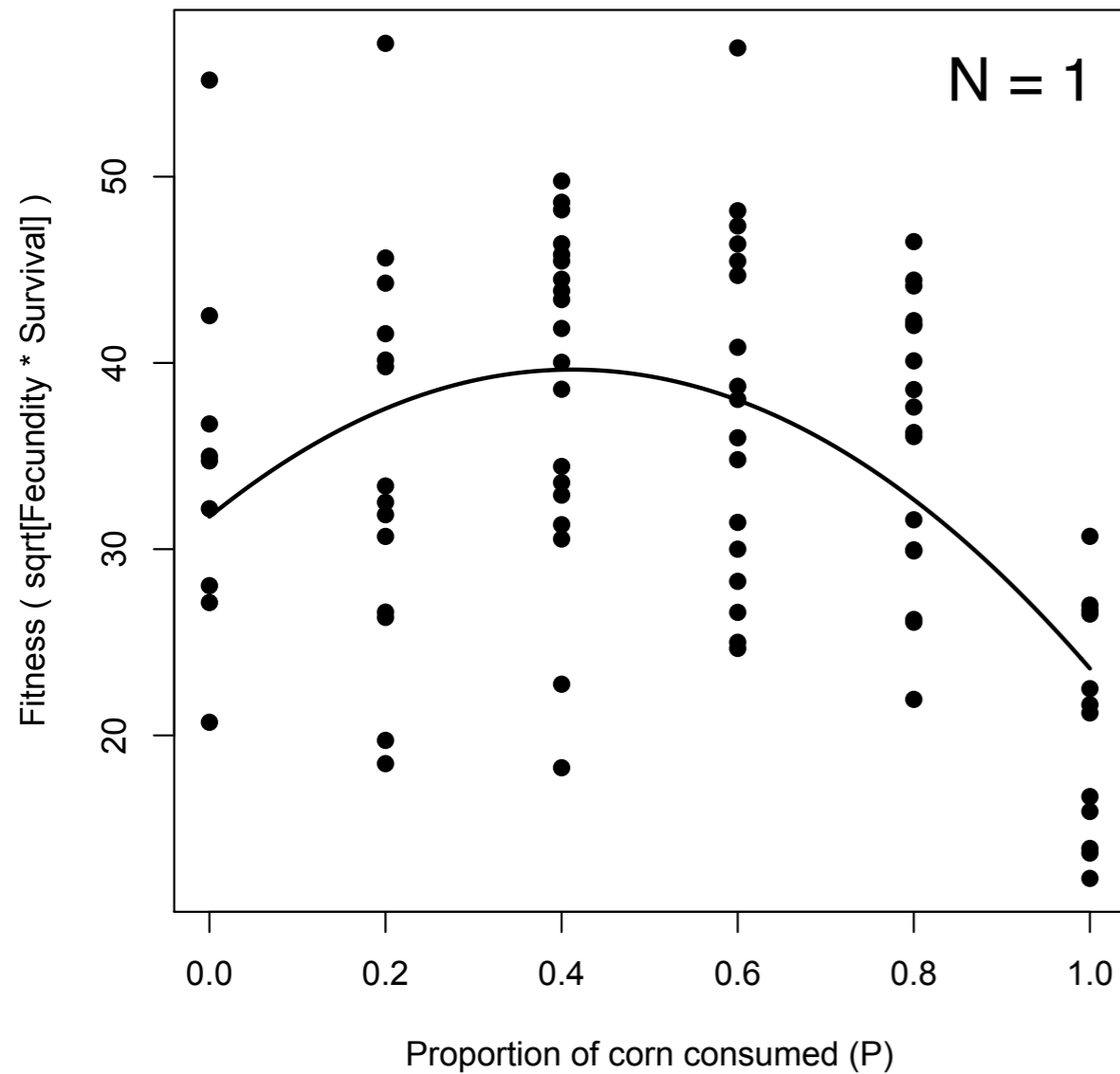
Synergistic interaction between W and C

low density

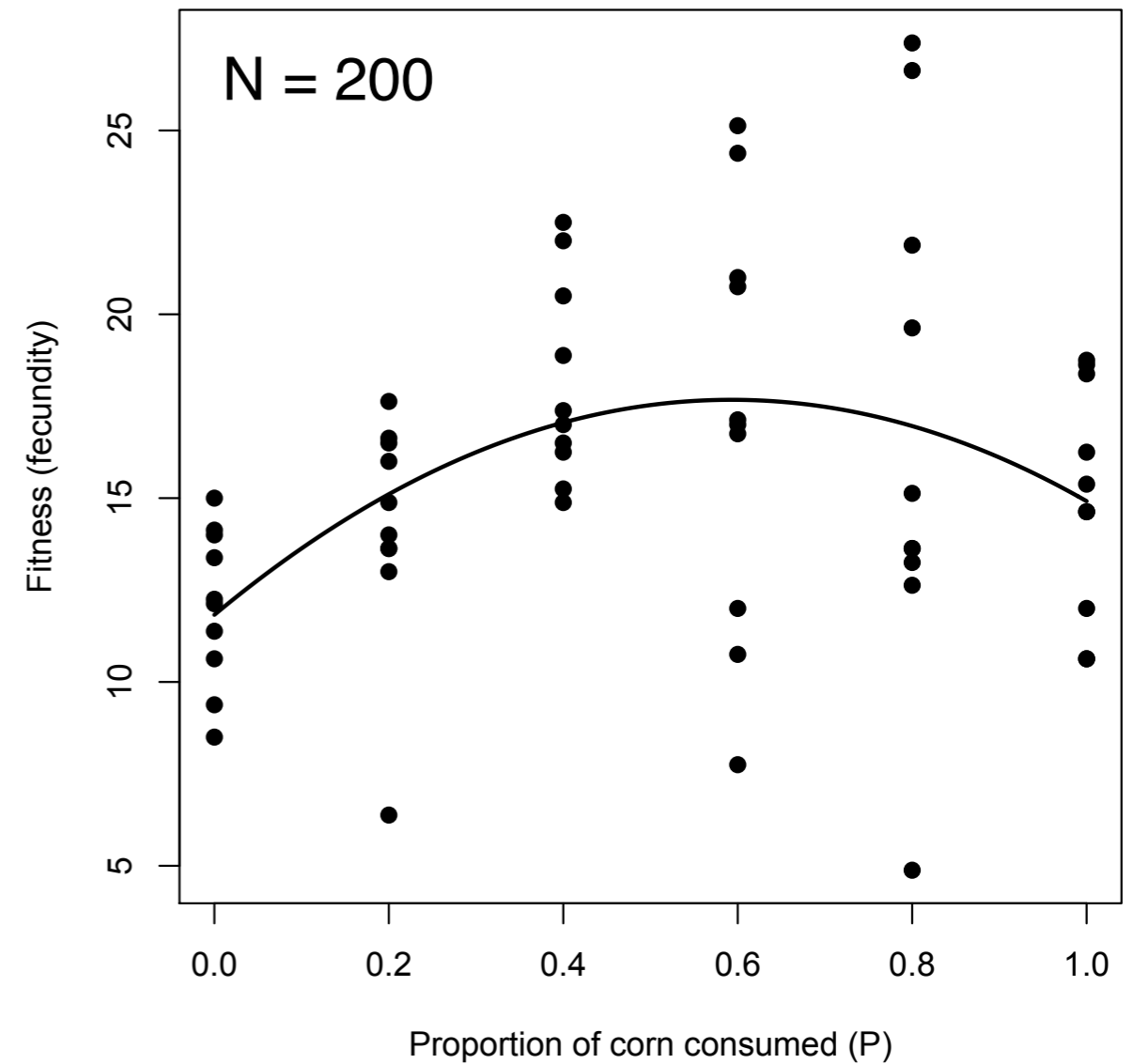


Synergistic interaction between W and C

low density



high density



quadratic term is density INDEPENDENT

(4) Test of assumptions: additive effects of resource use

Synergistic interaction between W and C

modification to basic model:

$$w = (1 - P) e^{[r_a'(1 + \alpha_a(N - 1)(1 - P))]} + P e^{[r_n'(1 + \alpha_n(N - 1)(P))]} + \boxed{P(1 - P)r_{an}}$$

Synergistic interaction between W and C

modification to basic model:

$$W = (1 - P) e^{[r_a'(1 + \alpha_a(N - 1)(1 - P))]} + P e^{[r_n'(1 + \alpha_n(N - 1)(P))]} + \boxed{P(1 - P)r_{an}}$$

- we fitted the value of r_{an} to match empirical findings (quadratic curves)
- combined with previous parameter estimates, we calculate optimal P
- the revised equation predicts non-zero values of optimal P at low density, BUT not the niche compression

Assumptions of the model

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Trade-offs associated with resource use

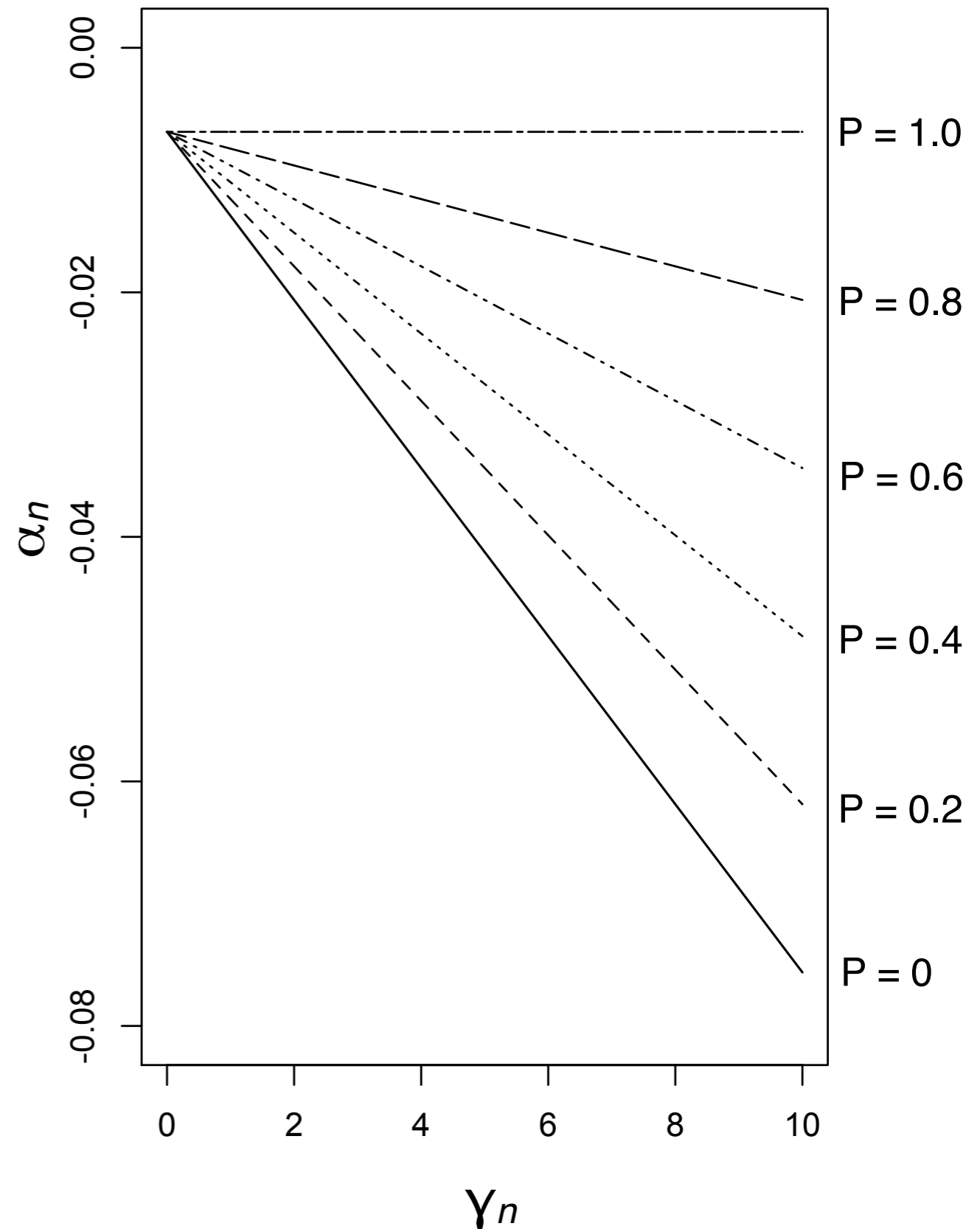
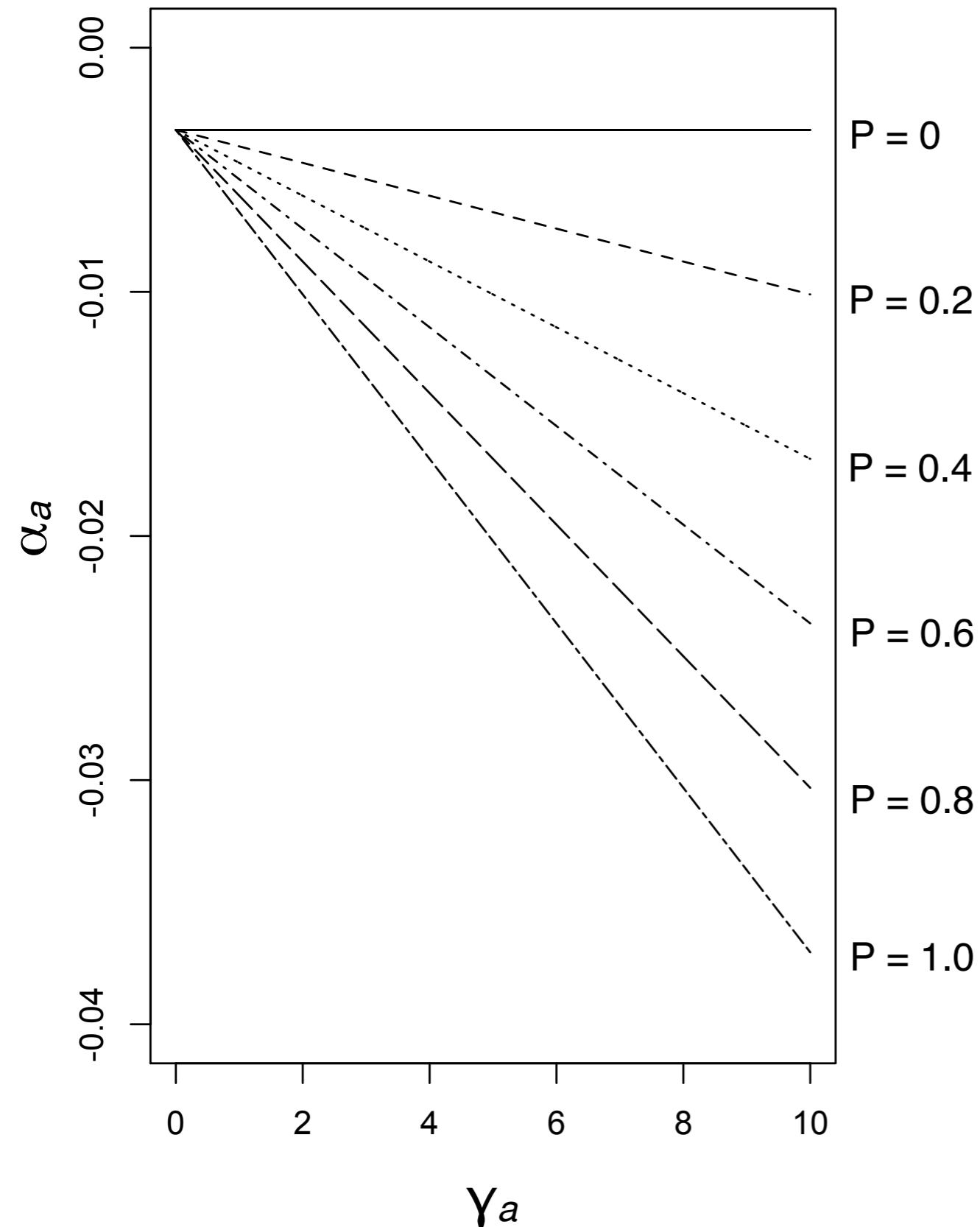
modification to basic model:

$$\alpha_a = \alpha_a'(1 + \gamma_a P)$$

$$\alpha_n = \alpha_n'(1 + \gamma_n(1 - P))$$

- α_i now is a function that inflates the competition coefficient on resource i at rate γ_i for each additional unit of the other resource j in the diet

Trade-offs associated with resource use



(4) Test of assumptions: no trade-offs in resource use

Trade-offs associated with resource use

modification to basic model:

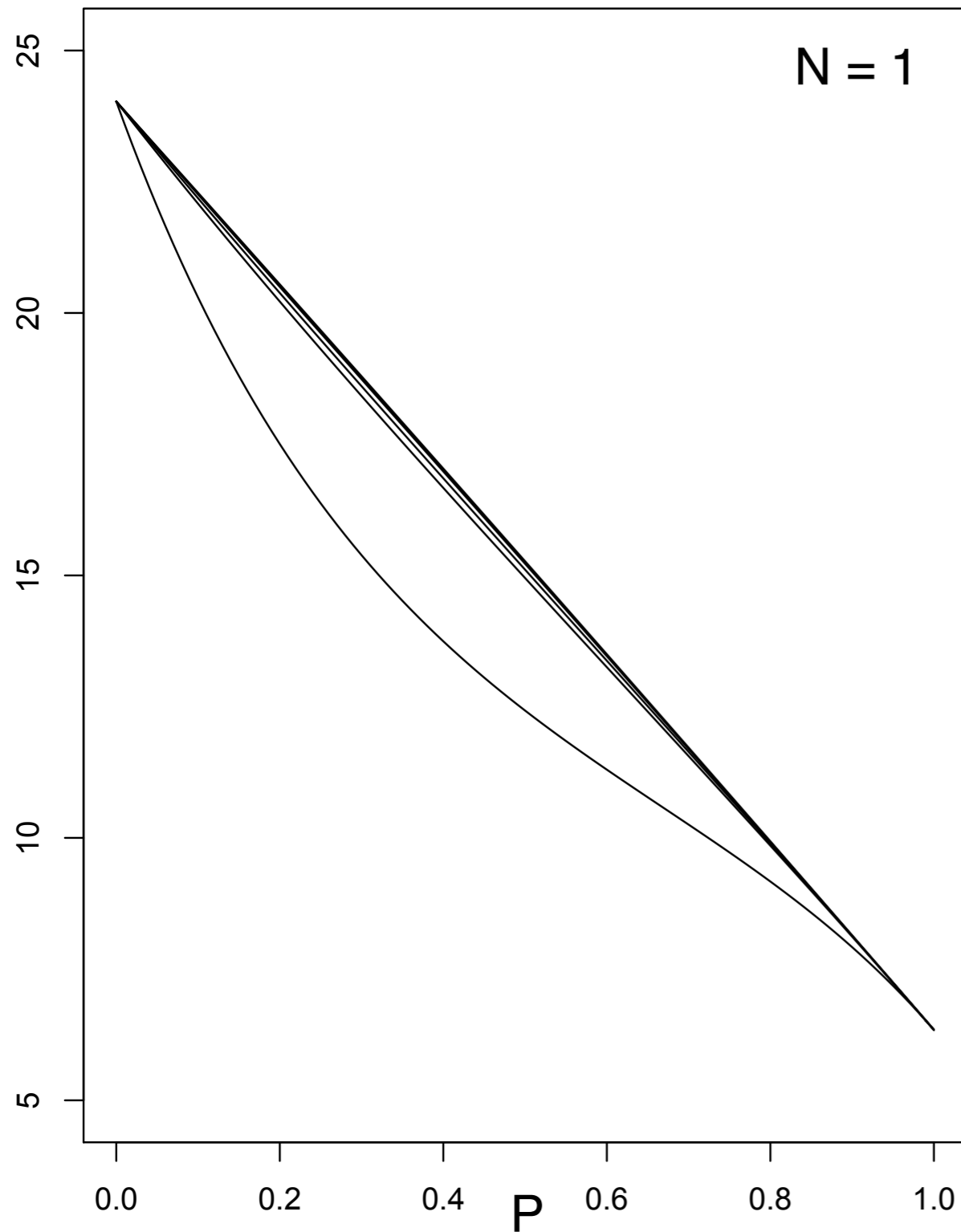
$$\alpha_a = \alpha_a'(1 + \gamma_a P)$$

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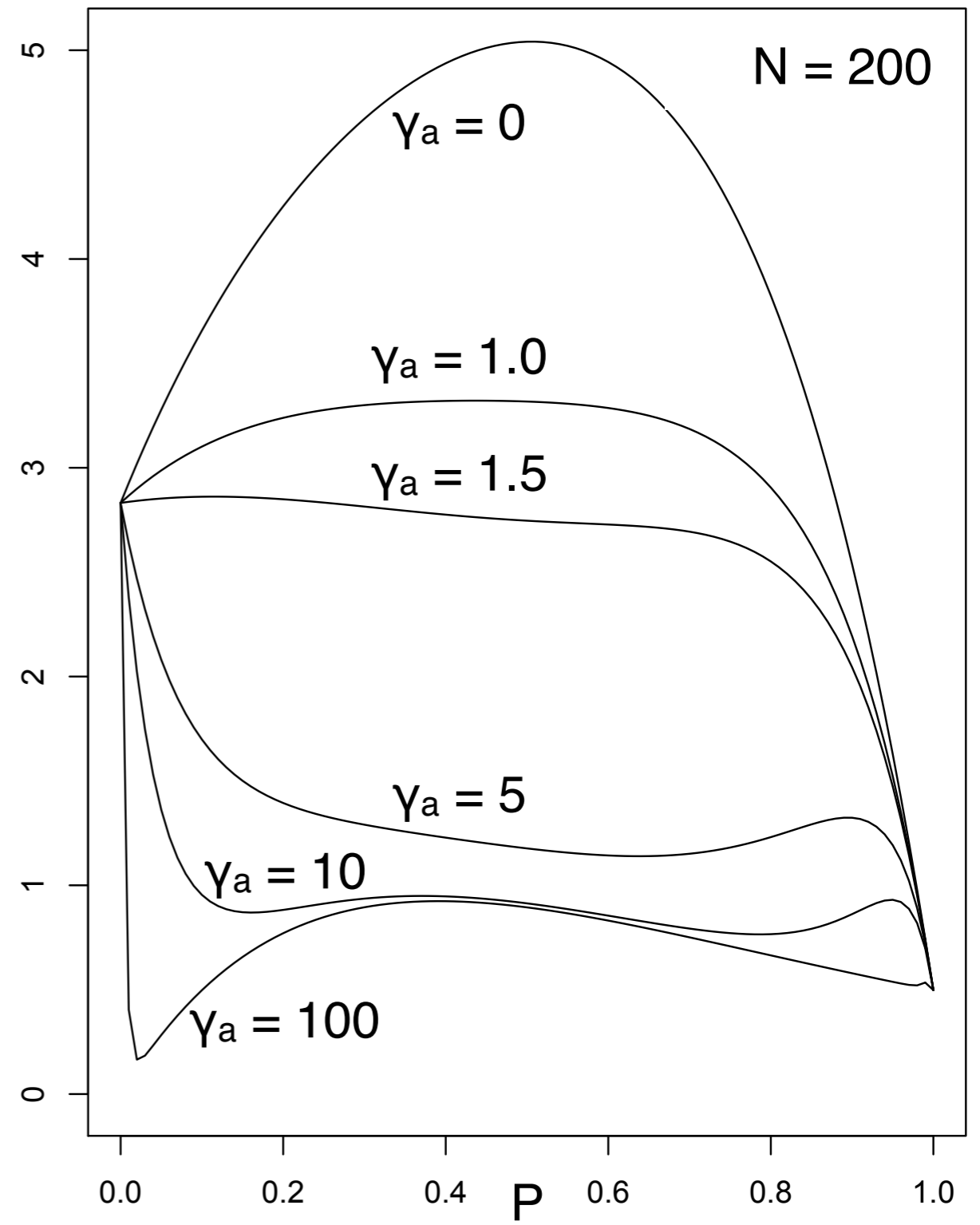
$$w = (1 - P) e^{[r_a'(1 + [\alpha_a'(1 + \gamma_a P)](N - 1)(1 - P))]} + P e^{[r_n'(1 + [\alpha_n'(1 + \gamma_n(1 - P))](N - 1)(P))]}$$

Effect of γ_a on fitness

low density



high density



(4) Test of assumptions: no trade-offs in resource use

Some conclusions

- Increased population density can lead to niche compression
- Niche compression in face of competition is not rare, but until now has remained theoretically unexplained
- Synergistic interaction can explain the benefit of using a combination of resource at low density, but fails to explain niche compression
- Trade-offs in resource use might explain niche compression with increasing competition in experimental populations of *Tribolium*
- Theories of competitive diversification and speciation would benefit from a more careful consideration of the potential different effects of population density on niche width and diversification

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Thank you!