Können Pinguine Schach spielen?

Jon Pitchford, Maths and Biology, York, UK.

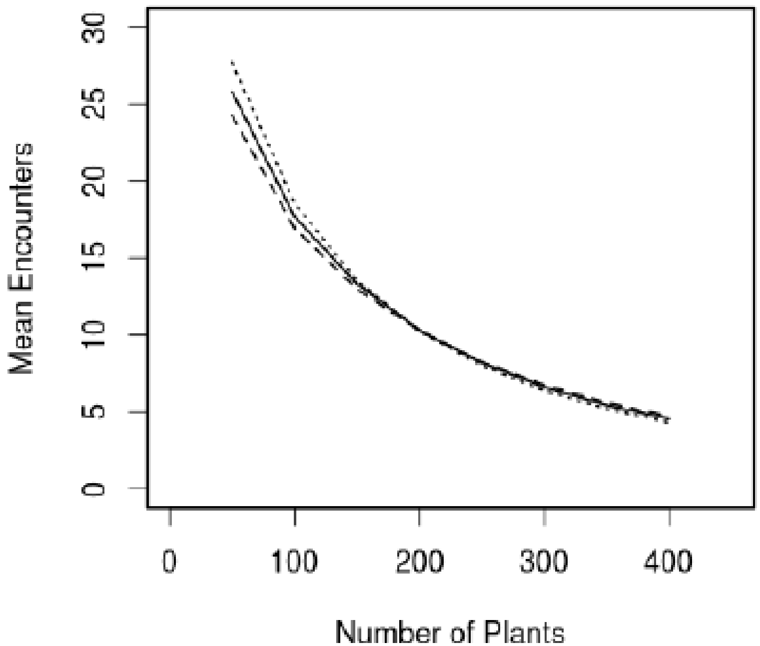
Sarah Collings and Marko Raseta (York), Simeon Hill and Eugene Murphy (British Antarctic Survey).

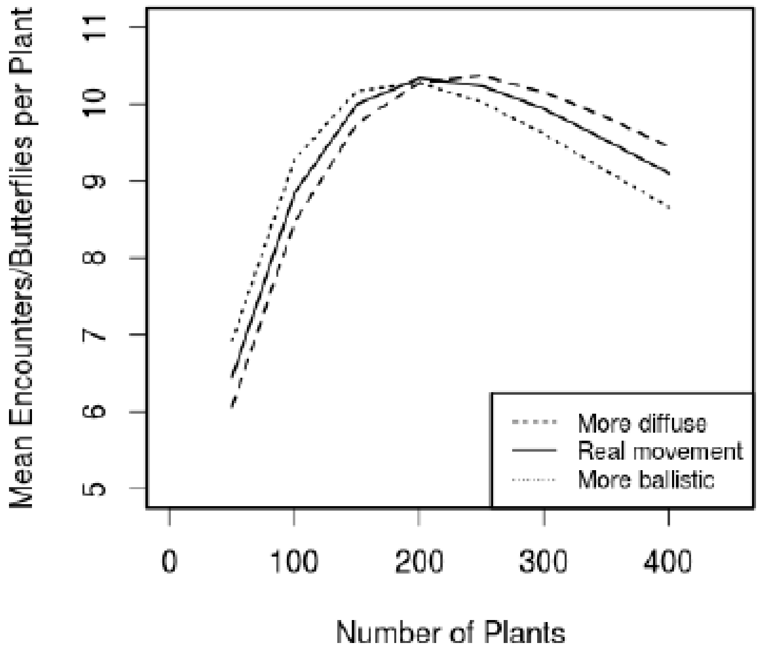
Two initial thoughts, from recent work with ecologists:

- Do the details of movement always matter?

- Real experimental results are “context dependent”. Our theoretical results are the same!

Do the details of movement matter?

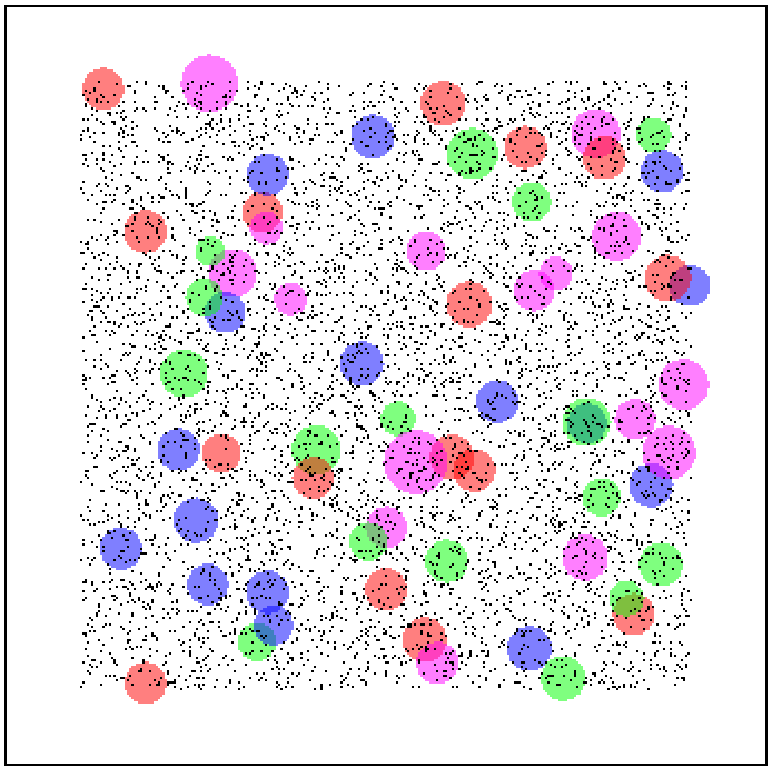




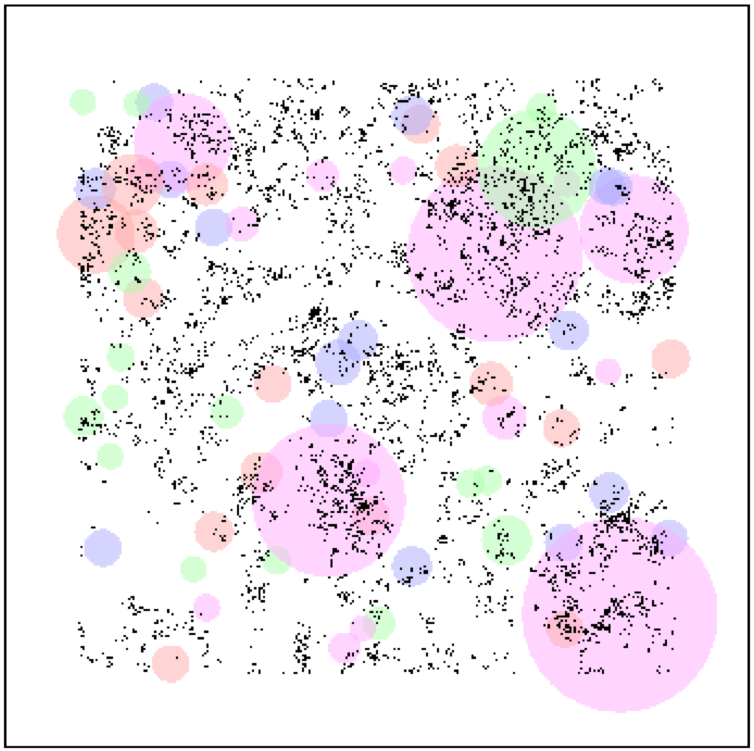
Preston, Forister, Pitchford, Armsworth, Ecological Complexity (to appear).

Context dependent results.

Uniform resources



Patchy resources



Croft, Hodge and Pitchford, AoB PLANTS (to appear).

Plan

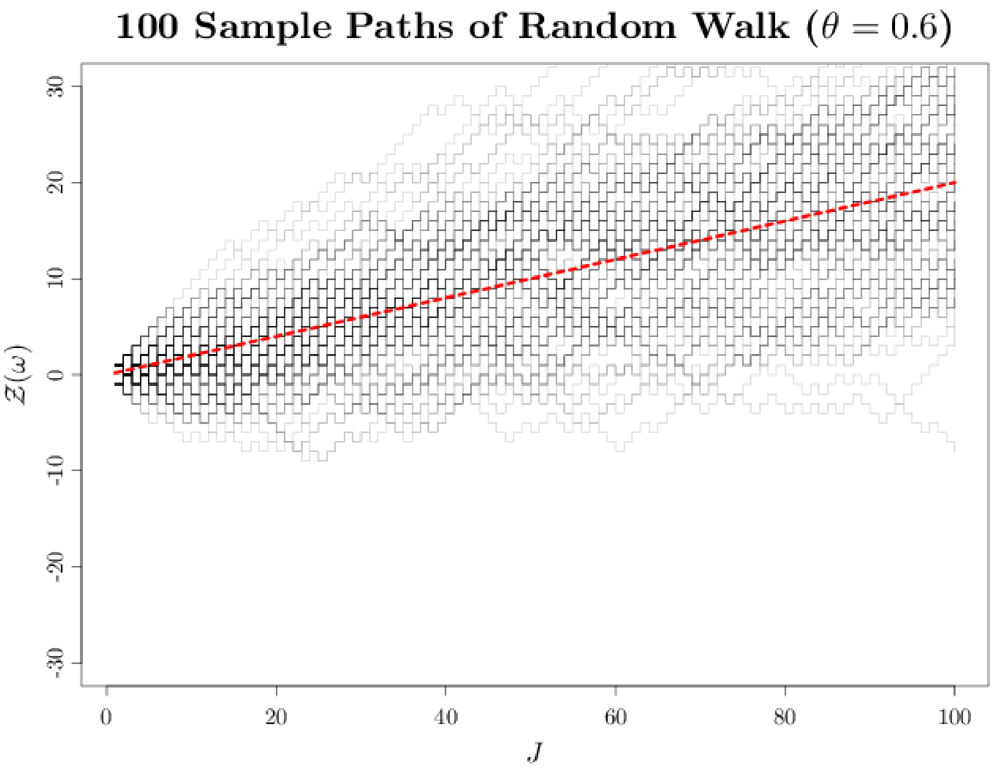
1. A very simple hitting time problem.

2. Some Antarctic biology.

3. Do penguins play chess?

1. A very simple hitting time problem.

Small, stupid, dead.



1. A very simple hitting time problem.

Consider the simplest deterministic growth model: fish of mass M grows at constant rate r, up to maturity at M_{mat}.

$$\frac{\mathrm{d}M}{\mathrm{d}t} = r, \qquad \text{with} \quad M(0) = 0,$$

A surviving fish reaches maturity at time

$$t^{\mathrm{d}}_{\mathrm{mat}} = \frac{M_{\mathrm{mat}}}{r},$$

so its probability of surviving to recruitment is simply

$$P_{\mathrm{mat}}(r, 0) = \exp\left(\frac{-\mu M_{\mathrm{mat}}}{r}\right)$$

Now take the SAME model, but add noise:

$$\frac{\mathrm{dM}}{\mathrm{d}t} = r + \sigma W(t)$$

where W(t) is a white noise process. M(t) then becomes a simple diffusion process (Brownian motion with drift):

$$\mathrm{M}(t) = rt + \sigma B(t),$$

and maturity time becomes a random variable:

$$t_{\mathrm{mat}} = \inf\{t > 0 : \mathrm{M}(t) = \mathrm{M}_{\mathrm{mat}}\},$$

$$f_{t_{\mathrm{mat}}}(t) = \frac{\mathrm{M}_{\mathrm{mat}}}{\sqrt{2\pi\sigma^2 t^3}} \exp\left\{-\frac{(\mathrm{M}_{\mathrm{mat}} - rt)^2}{2\sigma^2 t}\right\}.$$

Recruitment probability is then

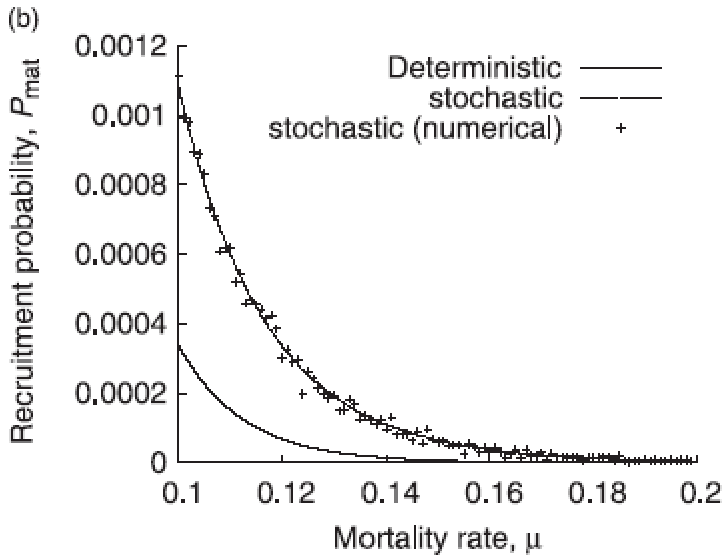
$$P_{\mathrm{mat}}(r,\sigma) = \int_0^\infty f_{t_{\mathrm{mat}}}(t)\exp(-\mu t)\mathrm{d}t$$

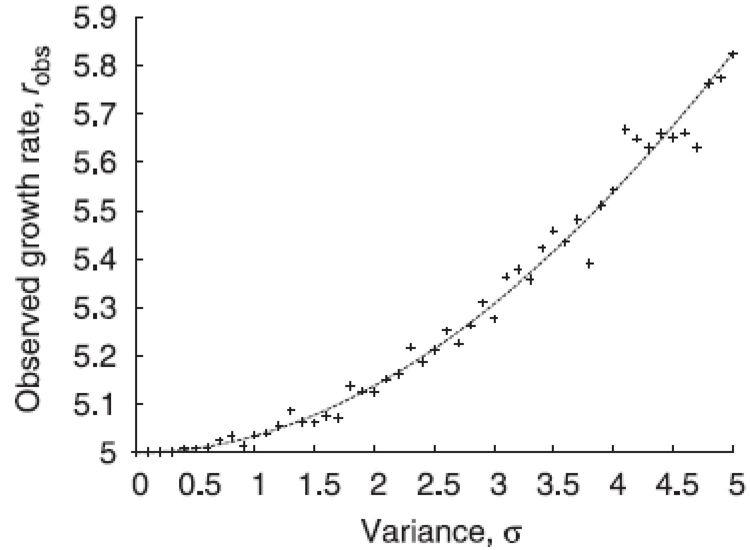
$$= \exp\left\{\frac{M_{\mathrm{mat}}r}{\sigma^2}\left(1-\sqrt{1+\frac{2\mu\sigma^2}{r^2}}\right)\right\}.$$

This looks very different to the deterministic. Is it useful?

$$\frac{P_{\mathrm{mat}}(r,\sigma)}{P_{\mathrm{mat}}(r,0)} = \exp\left\{\frac{M_{\mathrm{mat}}\mu^2\sigma^2}{2r^3} + O\left(\frac{M_{\mathrm{mat}}\mu^3\sigma^4}{r^5}\right)\right\}$$

i.e. stochasticity is ALWAYS BENEFICIAL, especially in a high mortality (or low growth rate environment).





Big effect on recruitment probability; noise is a good thing.

Big effect on inferred growth rate; you only measure the winners.

Adding “diffusion with jumps” results in a superdiffusive growth process; noise is an even better thing.

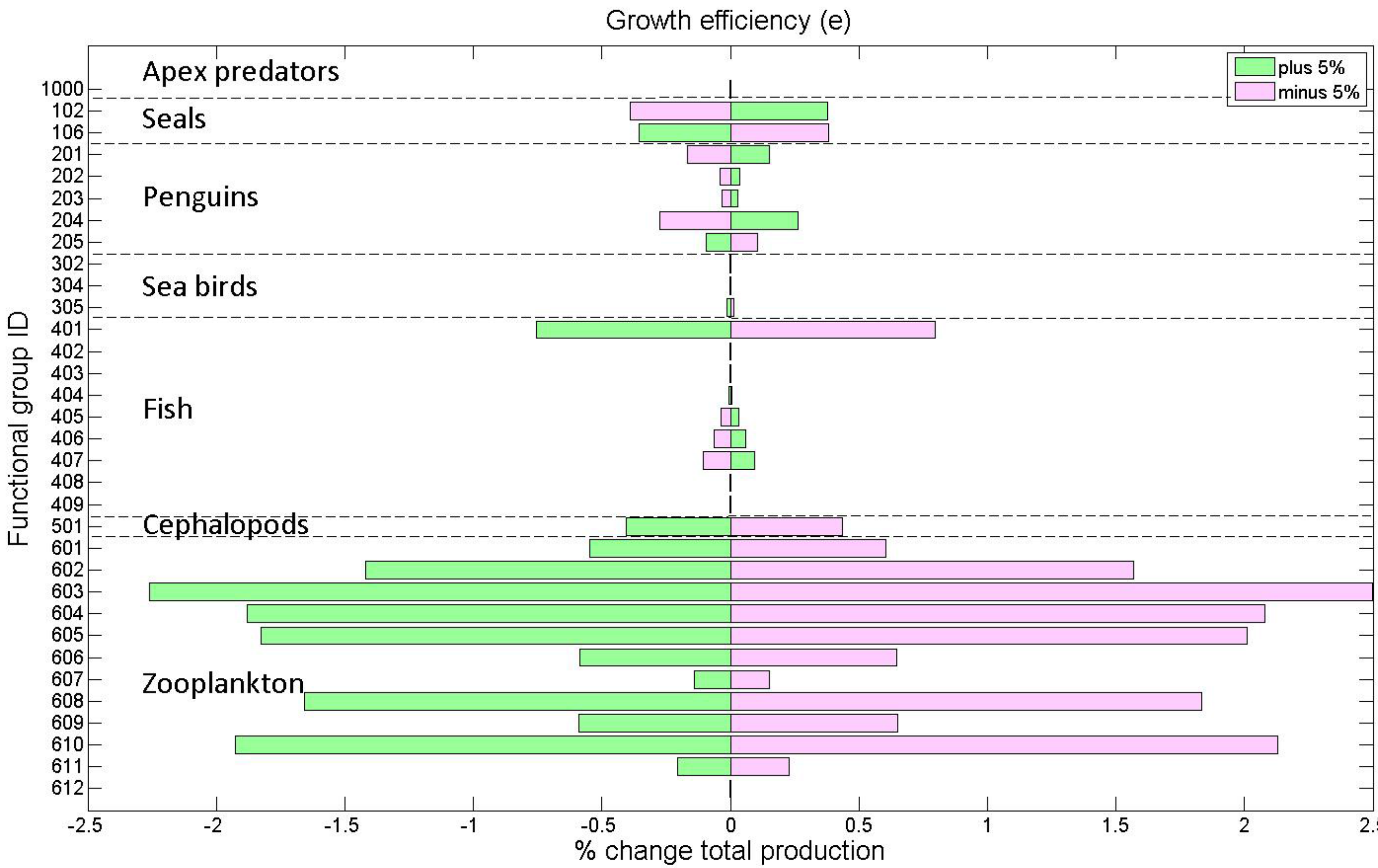
Pitchford, James and Brindley, (2005); Burrow, Baxter, Pitchford (2008)

2. Complex systems, Macaroni penguins and krill, and global carbon balance.

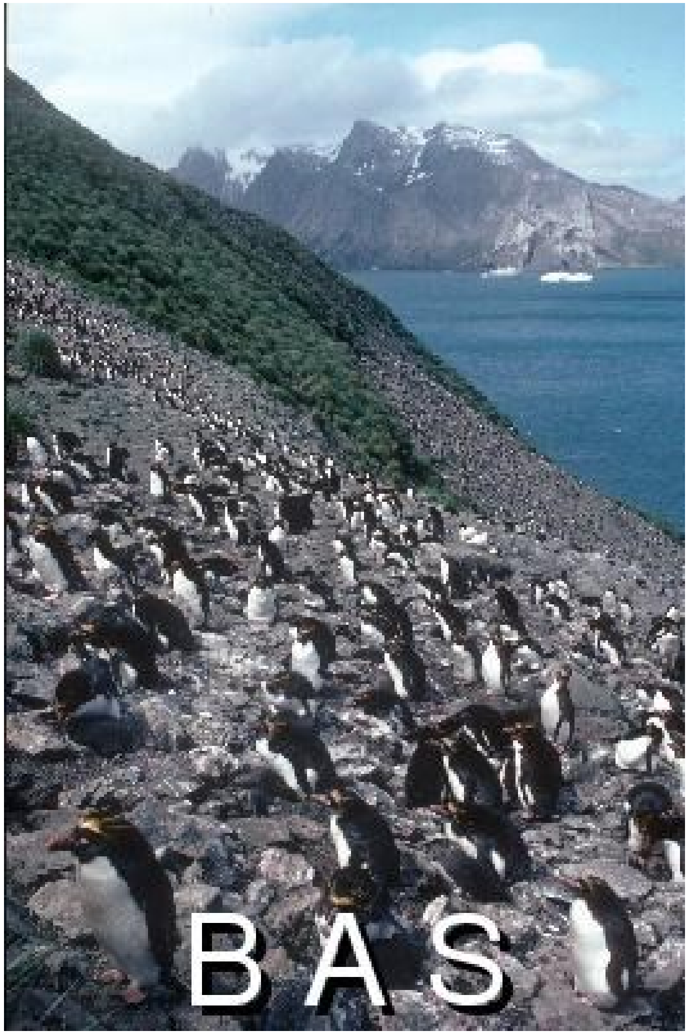
DOCKING the MACARONI.

Printed for Carington Bowles, Map & Printseller No 69 in St Pauls Church Yard, London. Published as the Act directs.

2. Complex systems, Macaroni penguins and krill, and global carbon balance.



My kids tell me my cooking is bad…



An excellent opportunity for ecological sampling.

- 1+ε eggs per year.
- Bi-parental care.
- Parents feed krill, or "other prey", to babies.
- 60 days to fledging.
- "Easy" to sample diet.

Empirical evidence:

- The first three weeks (brood period) is critical; mother forages while father stays at home.

- Penguins can be “krill specialists”, or not.

- Krill-rich diets cause bigger chicks.

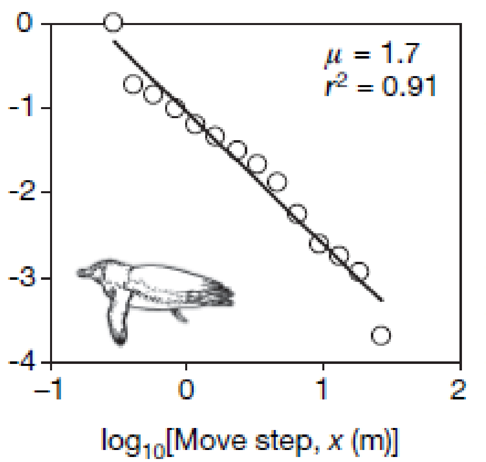
- Bigger chicks survive better.

- Krill availability is variable at small and large scales.

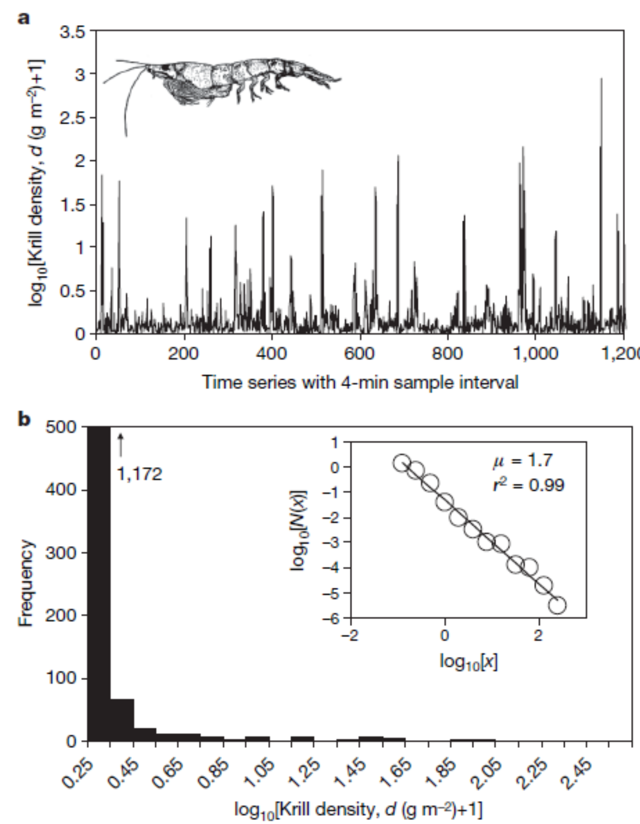
Krill can be hard to find

Useful questions

- How do penguins "specialise" to find krill?
- How will changes in krill recruitment and distribution affect this?



Sims et al. (2008)

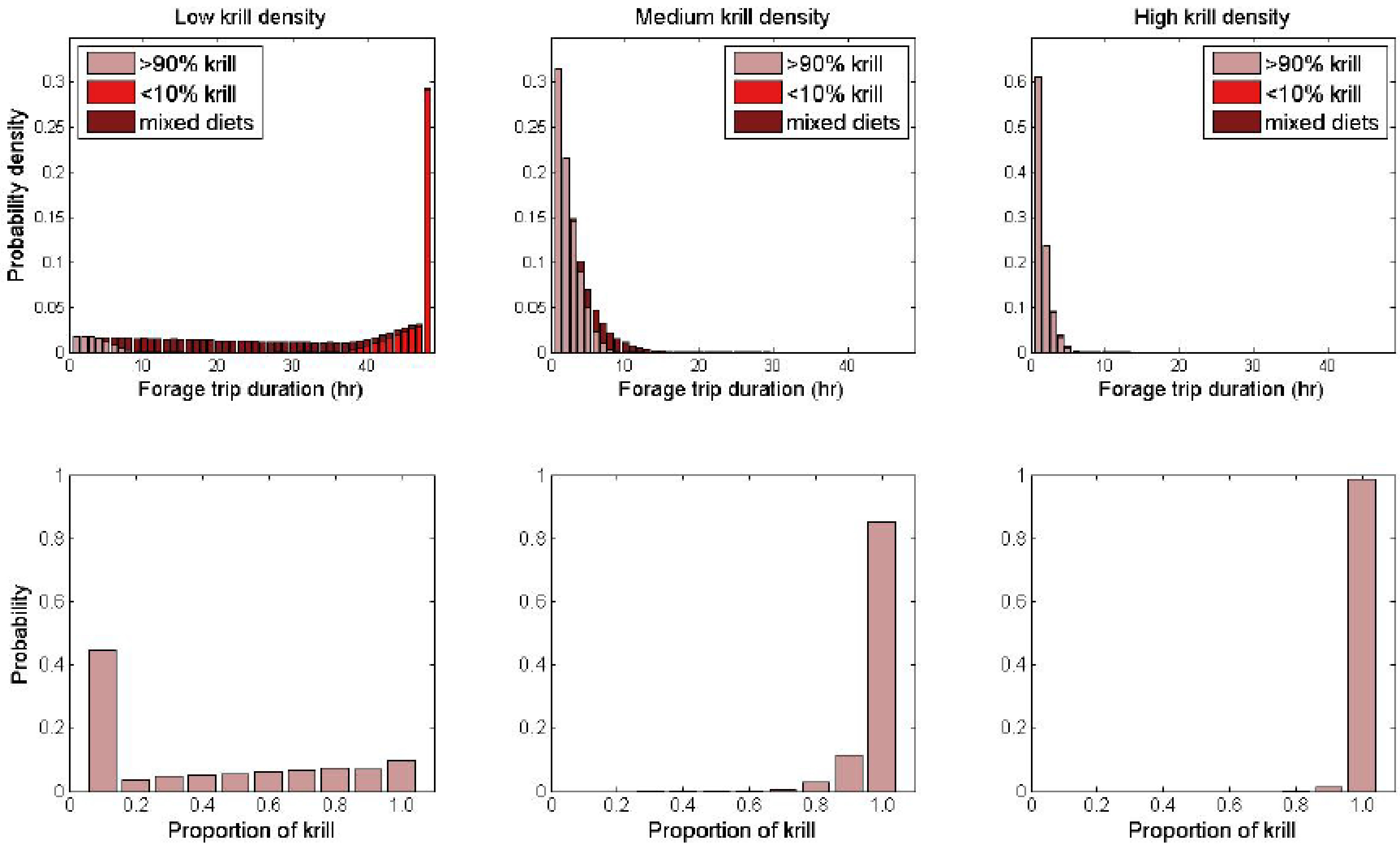


3. A very simple foraging model

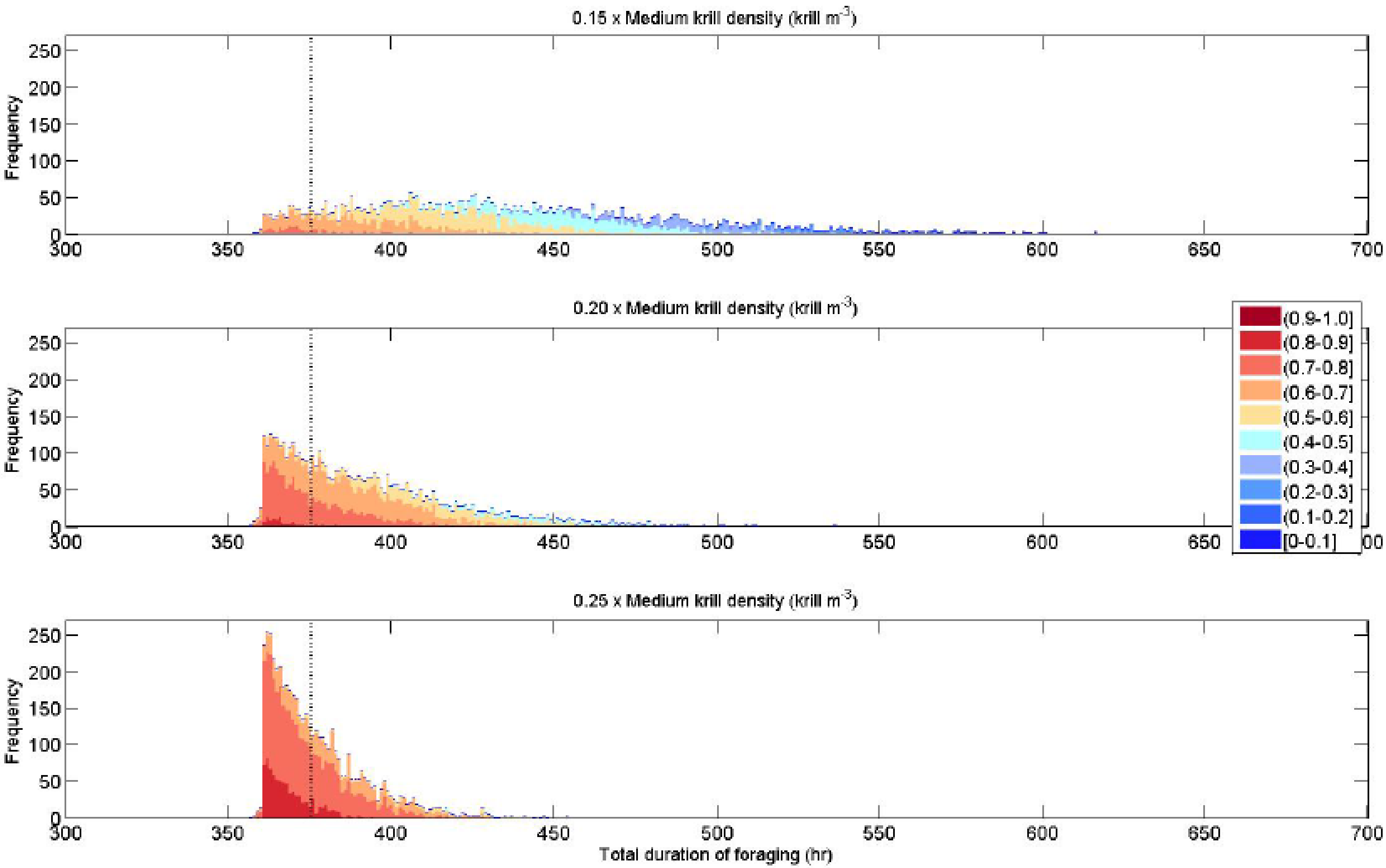
1. Predator foraging is not affected by its condition, weather events, competition from conspecifics or other predator species, or by its predators;
2. A predator forages alone, moves randomly in its environment and at a constant speed throughout a foraging trip;
3. A predator consumes two types of prey: Antarctic krill and alternate prey;
4. When the predator encounters prey it consumed it with a 100% success rate;
5. Time taken to capture and consume encountered prey (handling time) is small in comparison to search time and is, therefore, considered negligible;
6. Penguin foraging trips end when a predator is full (consumed n_m prey), or a maximum time limit (T_m = two days) has elapsed.

Alternatives: no krill aggregation, or krill form dense swarms.

Also details such as handling times, losing swarms, patchy alternative prey...



Apparent “specialisation” happens naturally as a consequence of krill swarming: bimodality in observed diets.

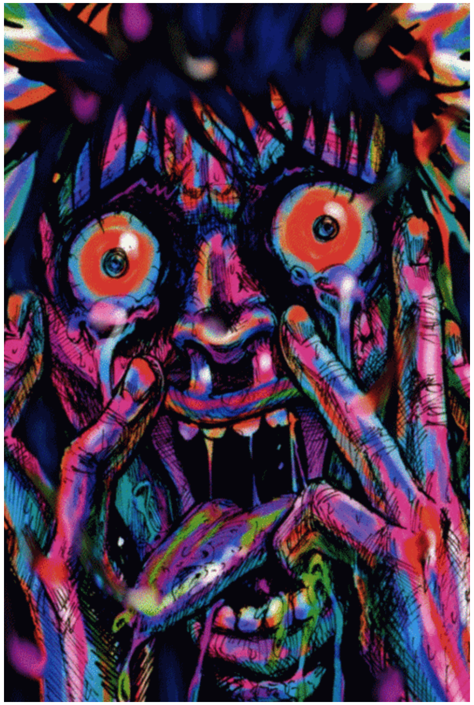


Encountering more krill on foraging trips (red shading) results in greater probability of success during the brood period (vertical line). The effect is large and nonlinear.

A toy model 2D random walk

"Taking LSD was a profound experience, one of the most important things in my life. LSD shows you that there's another side to the coin, and you can't remember it when it wears off, but you know it."

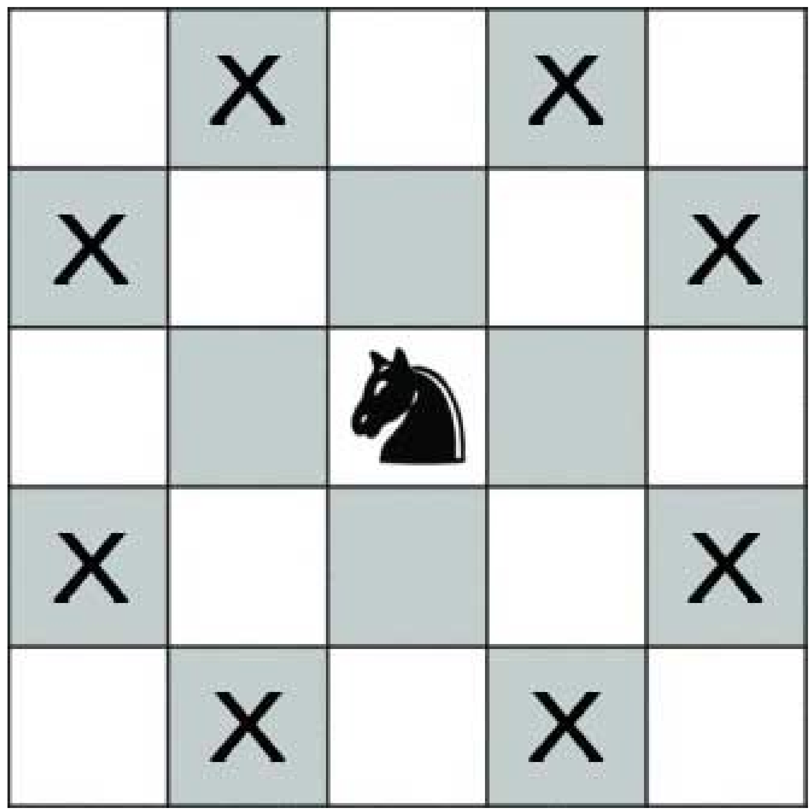
Good trip

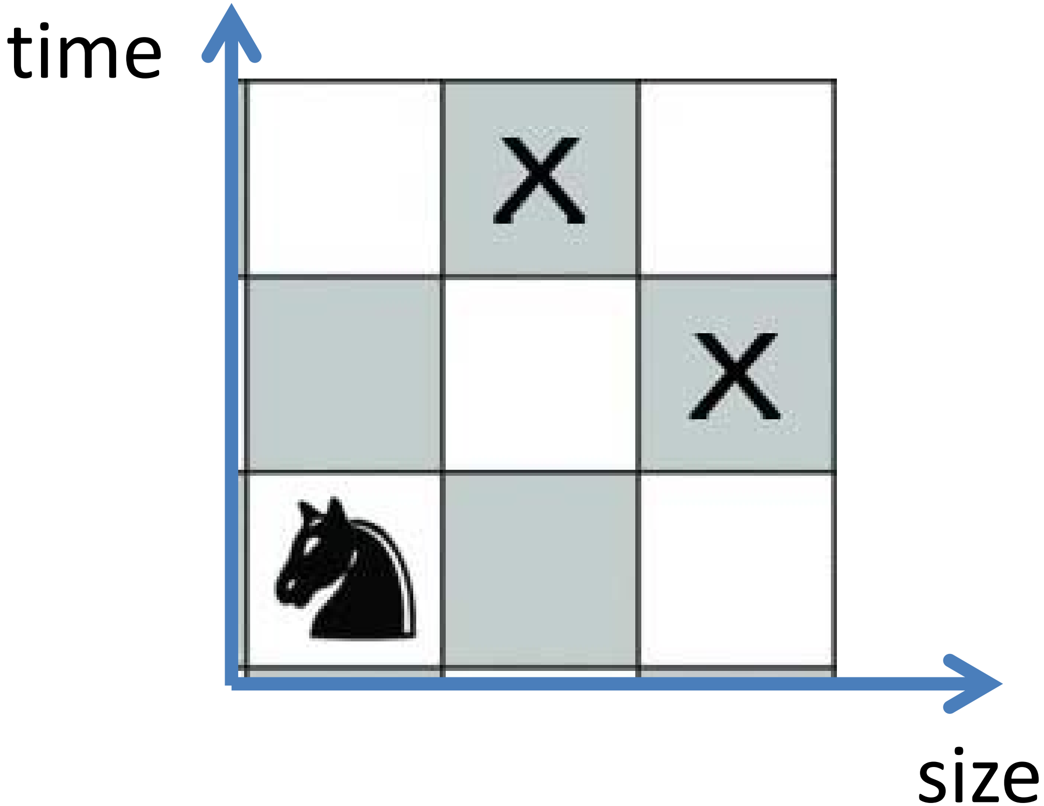


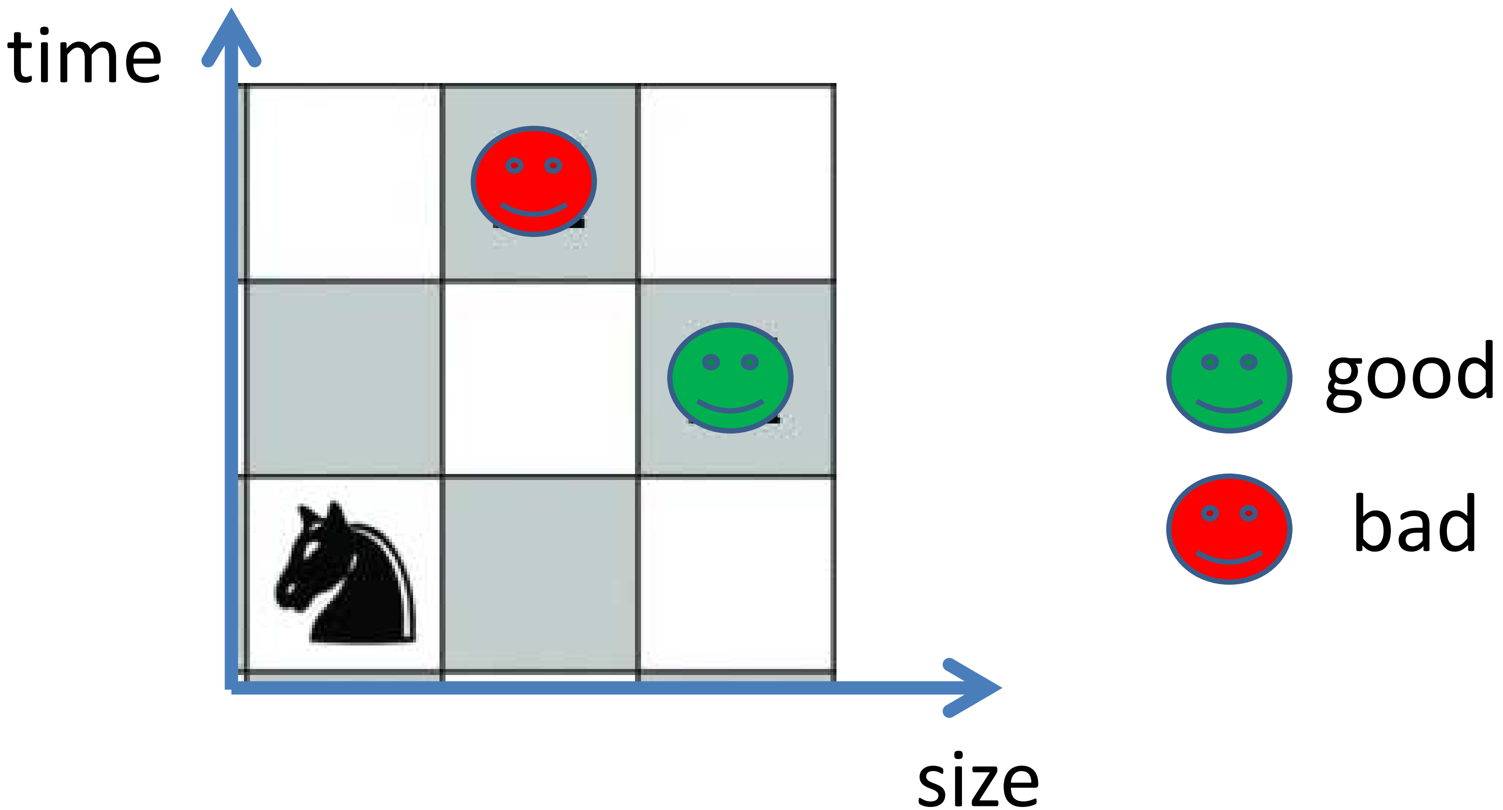
Bad trip

A toy model 2D random walk

"Doesn't time fly when you're having fun?"




time
X
X
size


time
size
good
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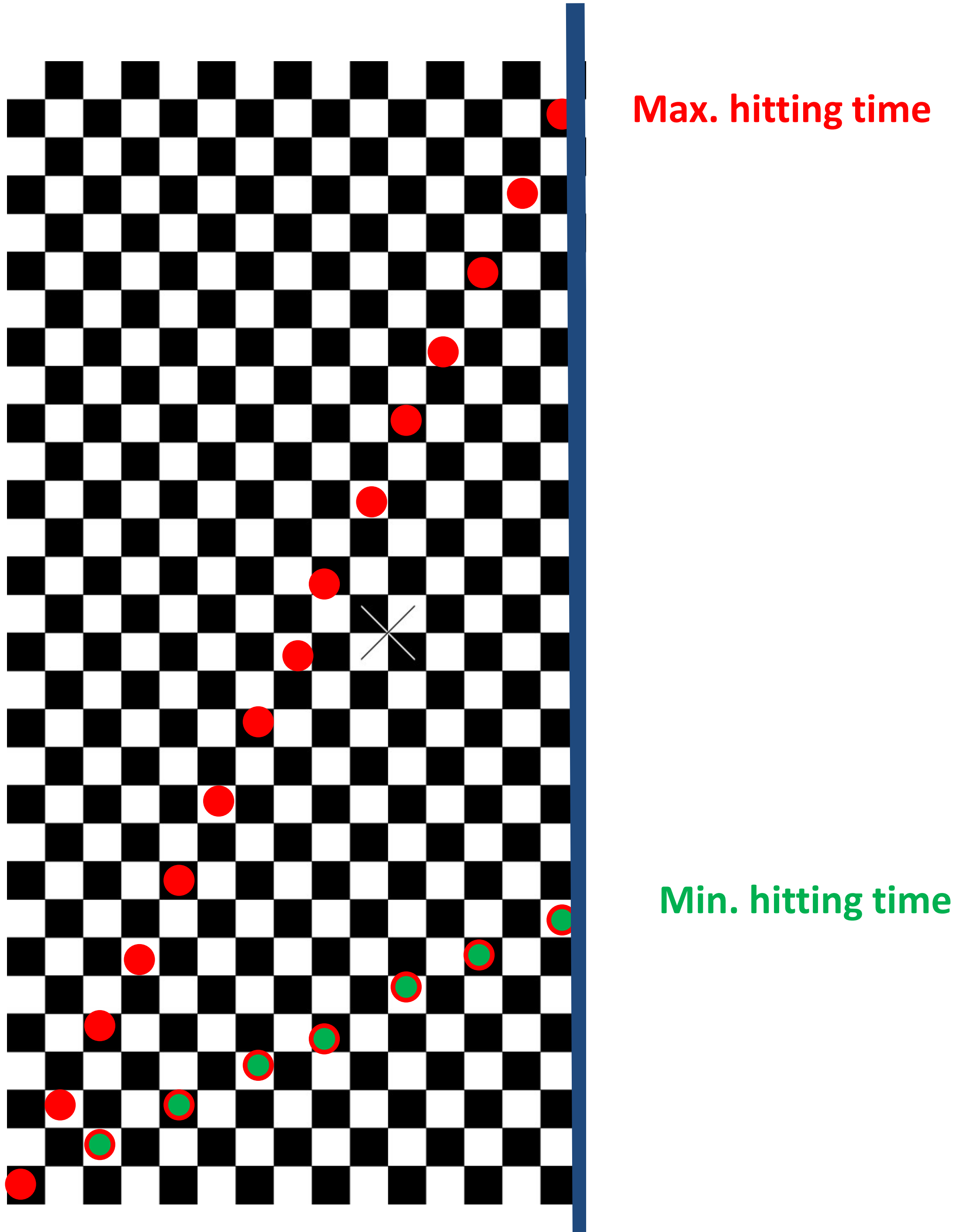
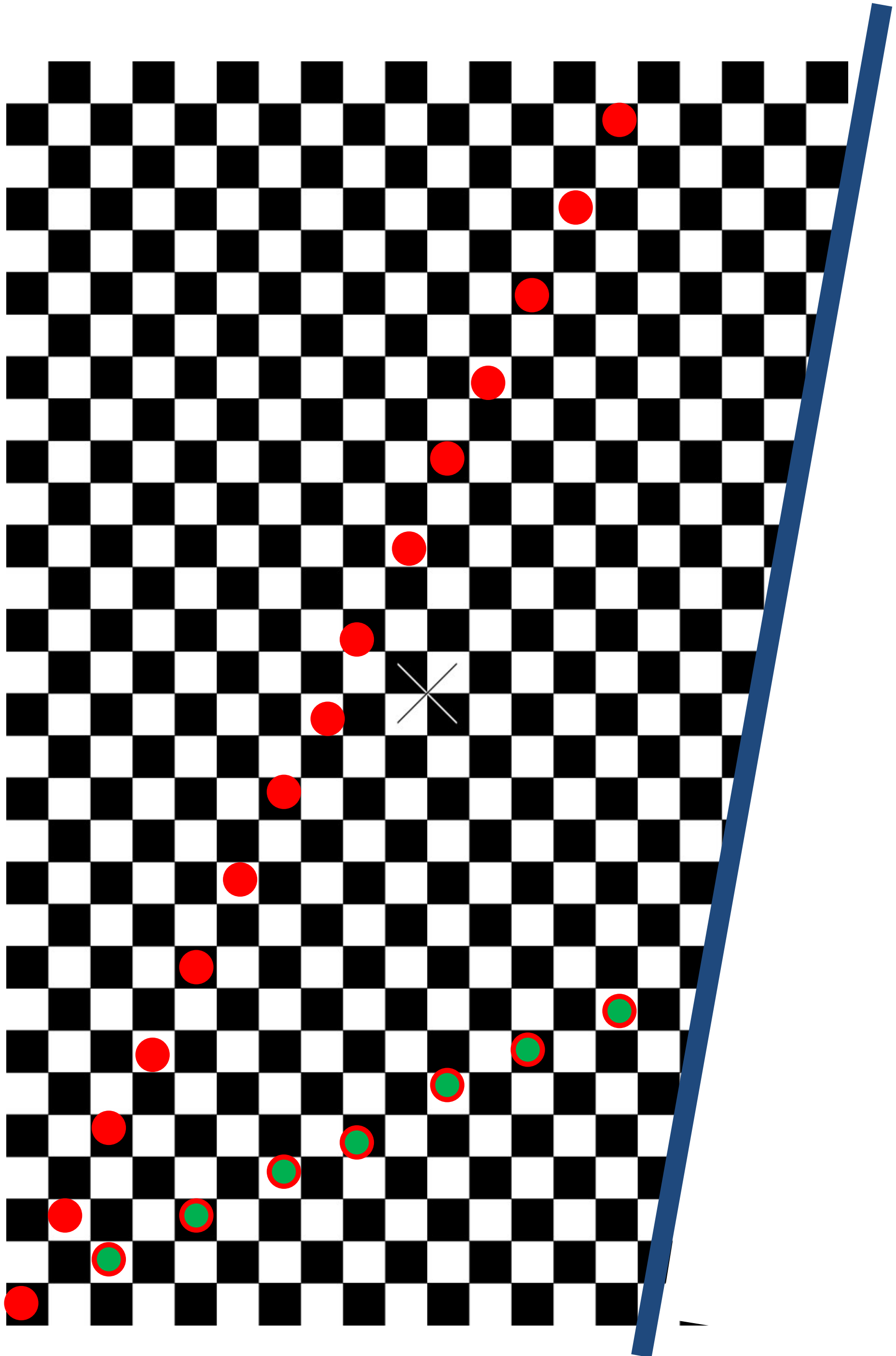
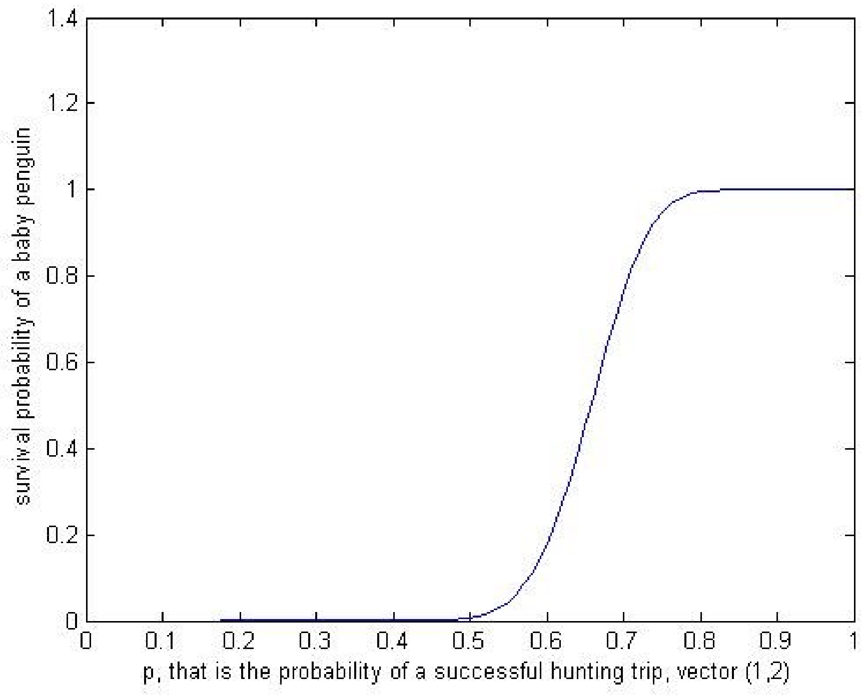

Max. hitting time
Min. hitting time



We can do this exactly, analytically.

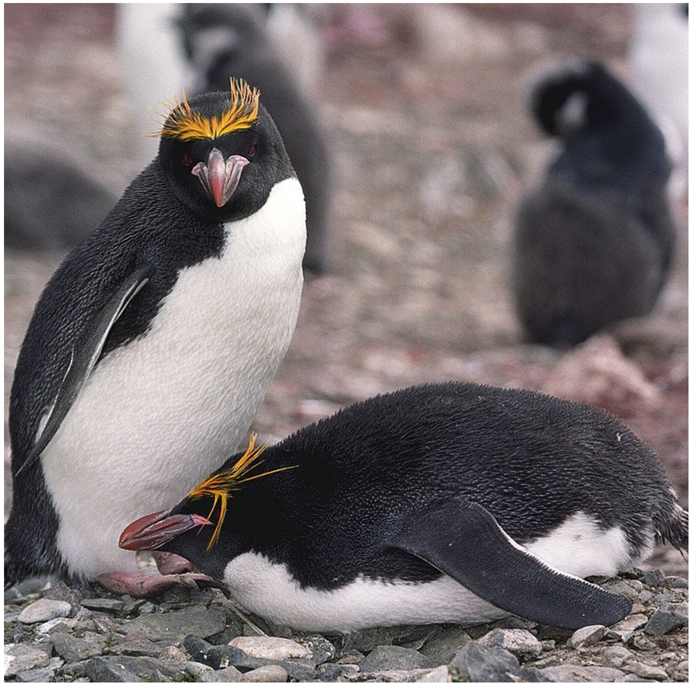
- The switch from “failure” to “success” emerges naturally.
- Key factors can be quantified.
- A framework to ask more interesting questions?



- But this is all “diffusive” theory… (or it will be).

Penguins: summary

- “Specialist” behaviour is just a simple consequence of patchy prey.
- Simple enough framework to look at “bigger” ecological questions, e.g. is krill timing more important than magnitude?
- Simple enough to look at the maths? (Vasily’s coupled jump models.)



Concluding thoughts

Lots of scope for better understanding between disciplines (not just physics and biology, but maths and statistics too).

- Dimensionality is important.
- Environment will matter.
- “Optimality” is subjective.
- All models are wrong, but some might be useful – it’s all “context dependent”.