Adaptive predator and prey movement rules in a spatial game

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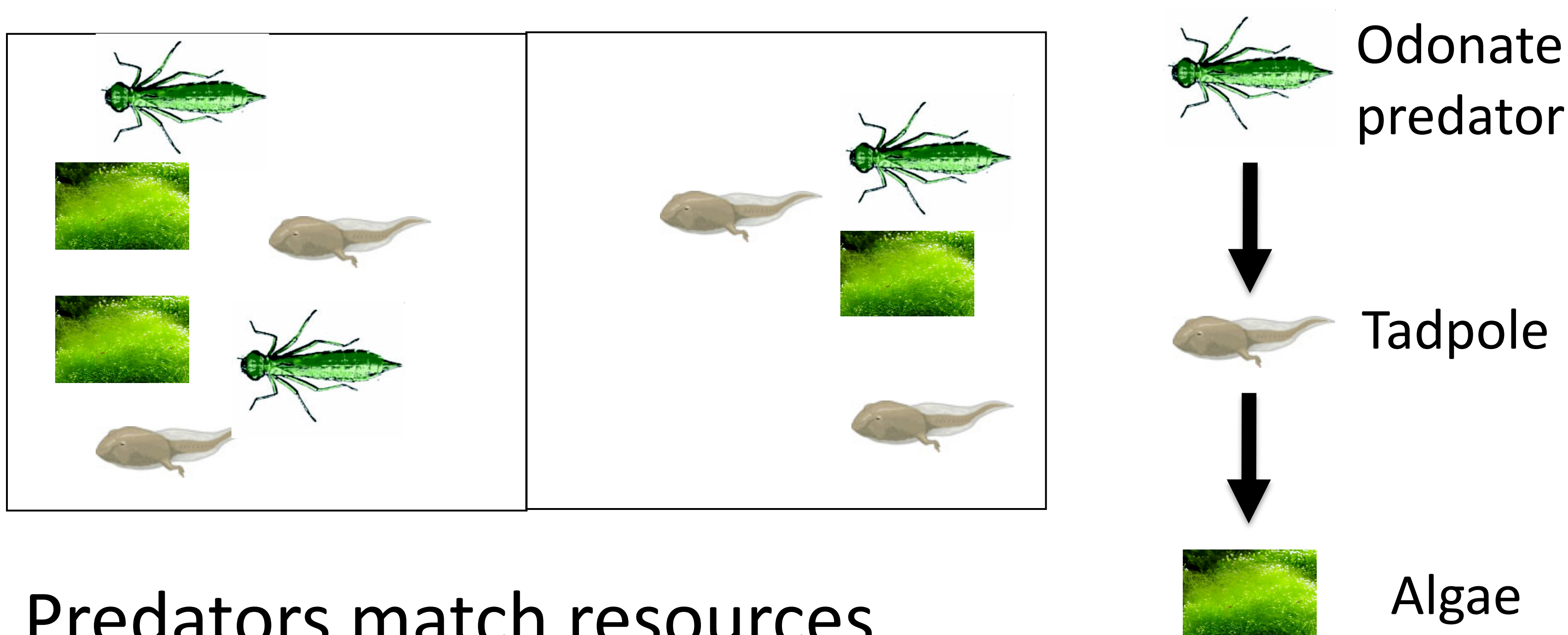
Convergence of two research areas

- Adaptive movements are being incorporated into ecological models (e.g. metacommunities, extinction risk, population dynamics, ect.)

- Expected predator and prey spatial distributions and movement rules when both are able to movement (spatial games)

Predicted predator and prey distributions

(Hugie and Dill (1994), Sih (1998), Luttbeg and Sih (2004), Flaxman and Lou (2009))

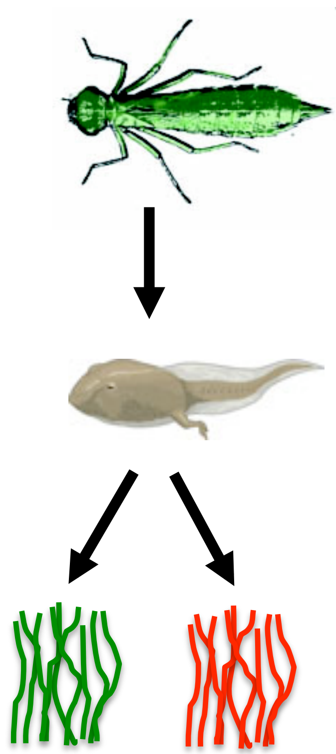


Predators match resources, prey uniform

Today's Plan

- Present an individual based model in which predator and prey movement rules evolve by a genetic algorithm
- What rules should predators and prey use when deciding to move?
- Do movement rules significantly affect population dynamics?
- Present some empirical support

Model system



Predator

Prey

Two resource types

Resources

- Two resource types
- Both grow logistically with equal growth rates and carrying capacities
- Resource type 1 gives prey twice more nutrition than Resource type 2,

$$nutri_1=2\ nutri_2$$

Patches

- 40 patches
- 20 patches contain Resource type 1 and 20 patches contain Resource type 2
- Spatially implicit

Prey

- Foraging gain in patch i with Resource type j = $nutri_j * r_i a_n$ (a is attack rate)
- No handling times or interference, but resource depletion

Predators

- Probability of a predator killing a prey in patch i = $n_i\, a_p$ (a is attack rate)
- No handling times or interference

Death and reproduction

- Probability of death each time step (0.1 for predators, 0.05 for prey)

- Reproduce when cumulative foraging gains exceed a threshold, offspring randomly placed in random patch

- Genetic algorithm, rule parameters passed to offspring; mutation and recombination occurs

Movement between patches

- Prey and predators free to move between patches
- No movement costs
- All have perfect information about current distributions of resources, prey and predators

Alternative movement rules for prey and predators

- No movement
- Random movement
- Instant fitness movement
- Multifactor movement (Full model)

Alternative rule: prey random movement

$$P_{ni} = b_{0n}$$

the probability that individual n switches to patch i

b_{0n} values evolve by a genetic algorithm

Alternative rule: prey instant fitness

$$P_{ni} = b_{0n} + b_{kn}\Delta_{k_i}$$

base

difference in prey fitness

$$\Delta_{k_i} = k_i - k_{\text{current}}$$

b values evolve by a genetic algorithm

Alternative rule: Multifactor prey movement

Φ: 0 or 1, on/off switch

Φ and b values evolve

$$
\begin{aligned}
P_{ni} = \; & b_{0n} + && \text{base} \\
& \Phi_{nn} b_{nn} \Delta_{n_i} + && \text{\# prey} \\
& \Phi_{pn} b_{pn} \Delta_{p_i} + && \text{\# predators} \\
& \Phi_{fn} b_{fn} \Delta_{f_i} + && \text{prey foraging gains} \\
& \Phi_{wn} b_{wn} \Delta_{w_i} + && \text{predator fitness} \\
& \Phi_{kn} b_{kn} \Delta_{k_i} && \text{prey fitness}
\end{aligned}
$$

Alternative rule: Multifactor predator movement

$$P_{pi} = b_{0p} + \Phi_{pp} b_{pp} \Delta_{p_i} + \Phi_{fp} b_{fp} \Delta_{f_i} + \Phi_{wp} b_{wp} \Delta_{w_i} + \Phi_{kp} b_{kp} \Delta_{k_i}$$

b_{0p}	base
$\Phi_{pp} b_{pp} \Delta_{p_i}$	# predators
$\Phi_{fp} b_{fp} \Delta_{f_i}$	prey foraging gains
$\Phi_{wp} b_{wp} \Delta_{w_i}$	predator fitness
$\Phi_{kp} b_{kp} \Delta_{k_i}$	prey fitness

Move or stay?

- P_{ni} (or P_{pi} for predators) calculated for each patch
- Largest value used
- Movement stochastically determined

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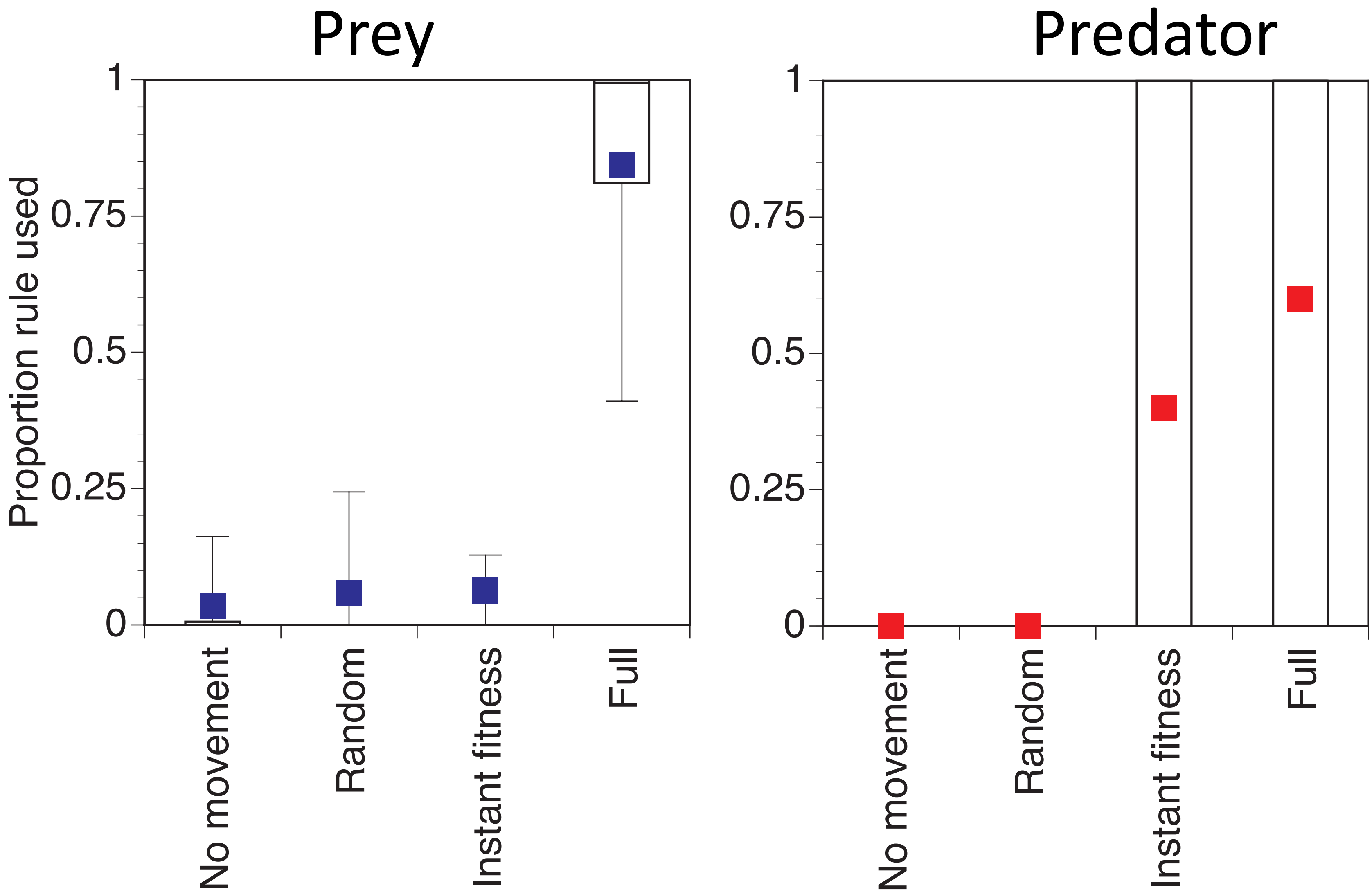
Timing of movement decisions and foraging

- Sequential movement with immediate foraging
  - each time step each individual in random order moves or does not and then forages

Tournament: which rules will they use?

- Start with 800 prey
  - equal numbers using No Movement, Random Movement, Instant Fitness, and Full model
- 480 predators (equal numbers of 4 rules)
- Parameters values passed to offspring with some mutation and recombination
- Run for 10,000 time steps
- 20 replicates

Sequential: Final rules used in Tournament

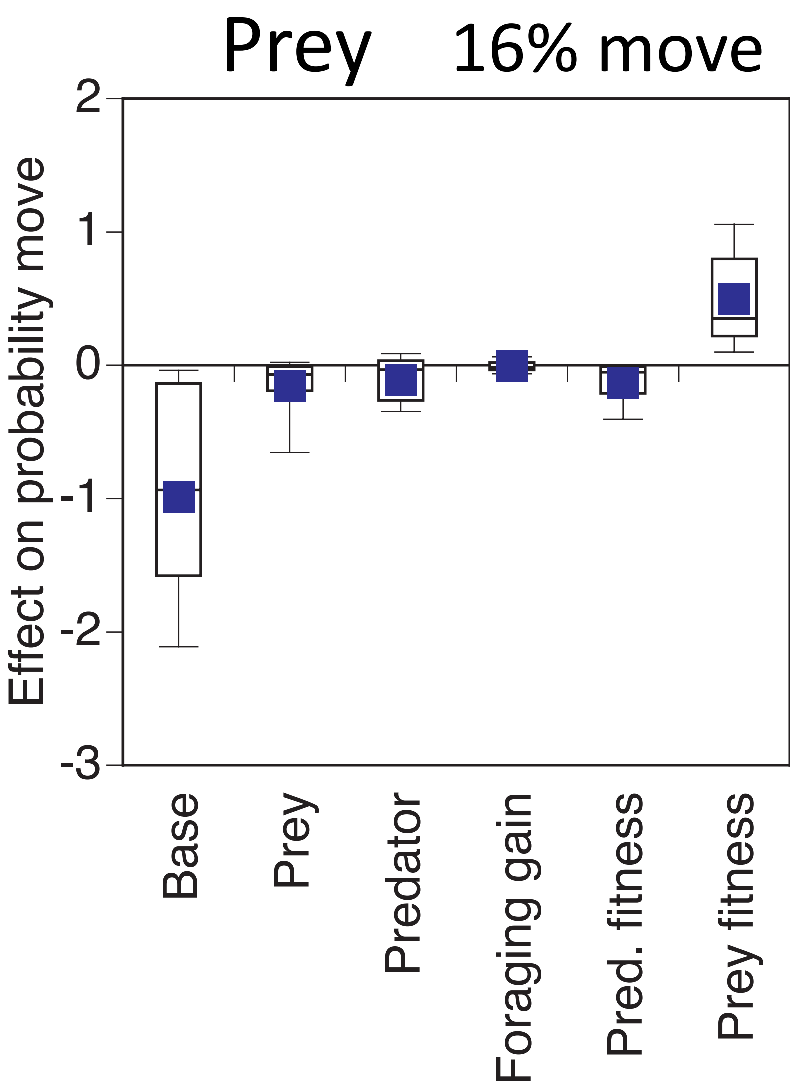


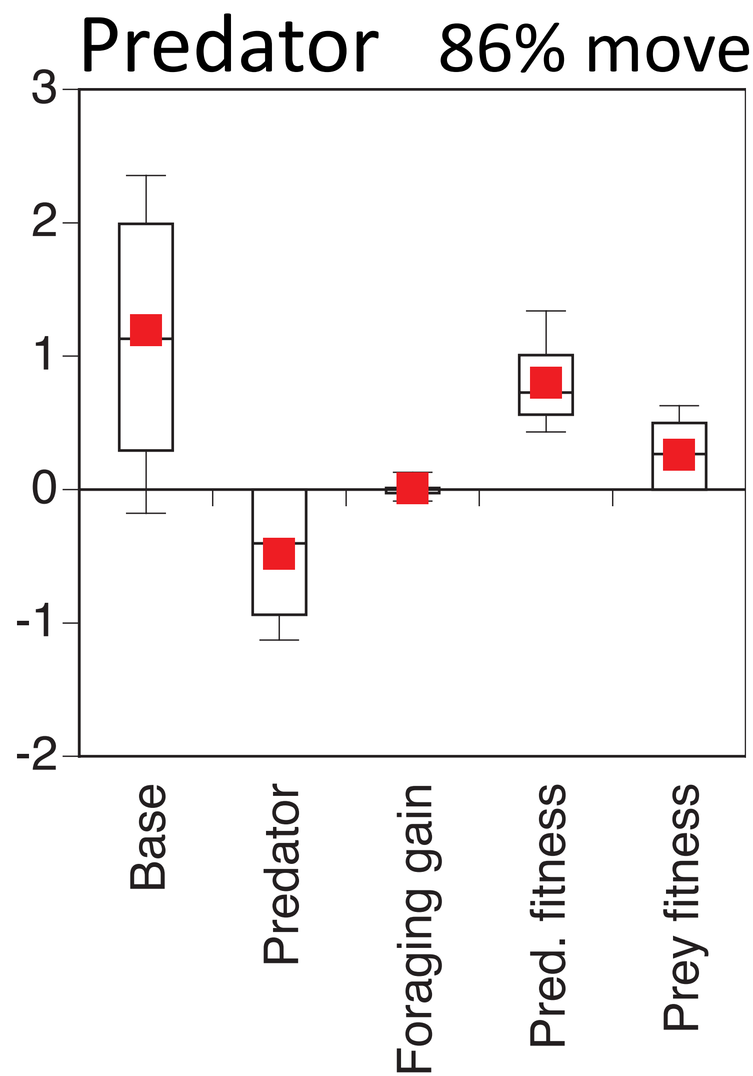
Full Prey movement rule (probability of switching patches)

$$P_n = b_{0n} + \Phi_{nn} b_{nn} \Delta_n + \Phi_{pn} b_{pn} \Delta_p + \Phi_{fn} b_{fn} \Delta_f + \Phi_{wn} b_{wn} \Delta_w + \Phi_{kn} b_{kn} \Delta_k$$

- b_{0n}: base
- $\Phi_{nn} b_{nn} \Delta_n$: prey
- $\Phi_{pn} b_{pn} \Delta_p$: predators
- $\Phi_{fn} b_{fn} \Delta_f$: prey foraging gains
- $\Phi_{wn} b_{wn} \Delta_w$: predator fitness
- $\Phi_{kn} b_{kn} \Delta_k$: prey fitness

Sequential: Effects on probability of moving





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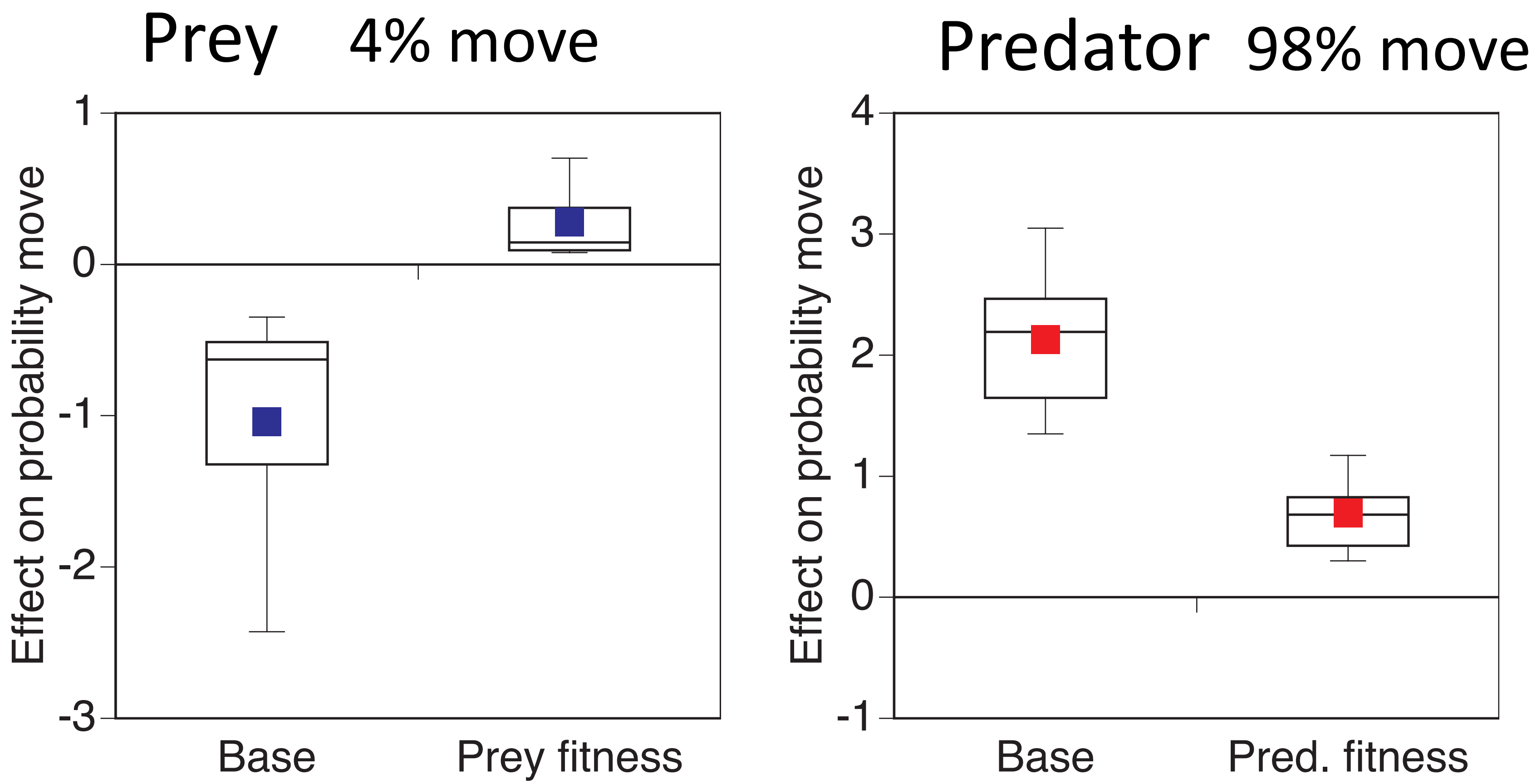
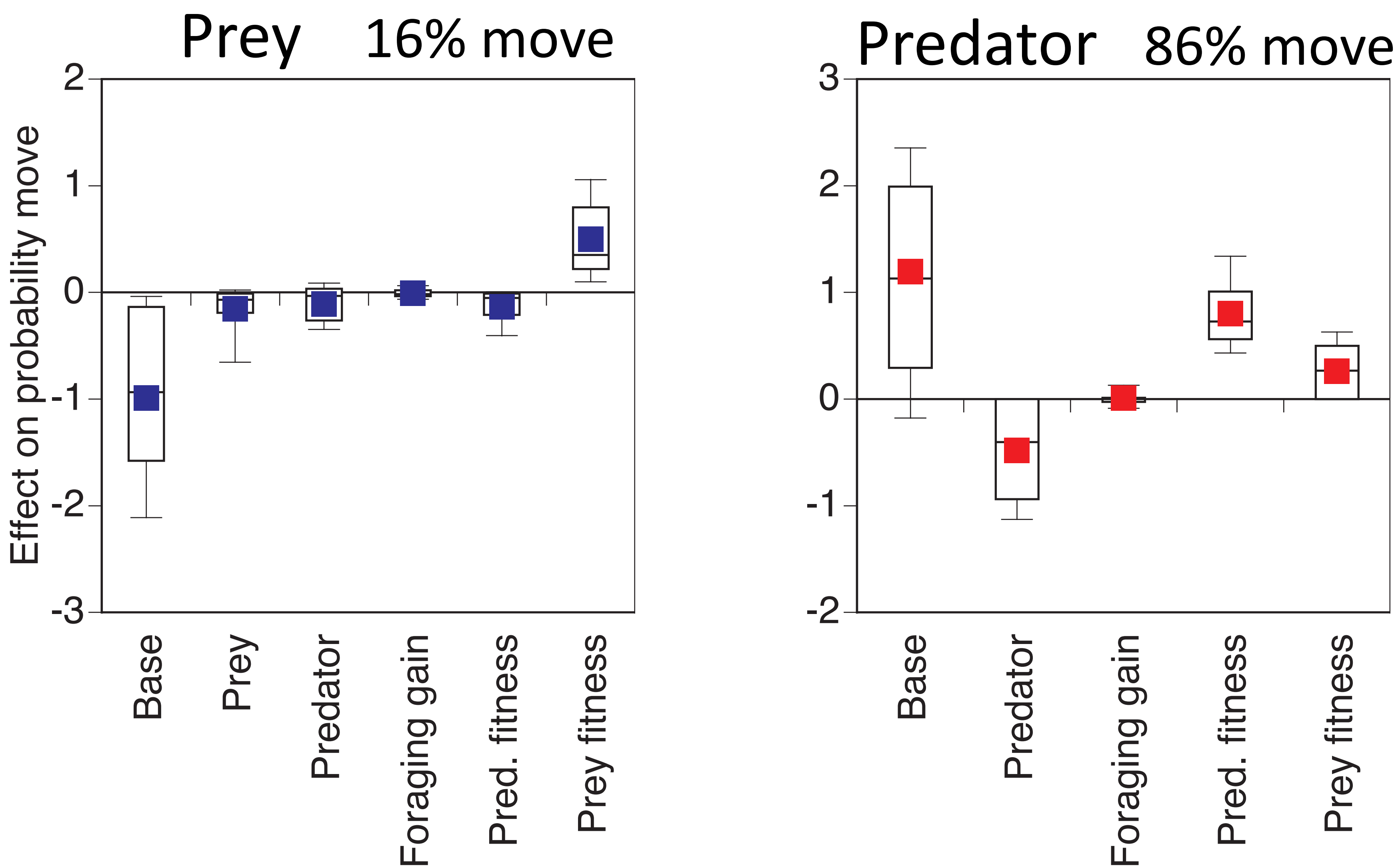
Comparing population dynamics

- Rules at end of Tournament
- Full model only
- Instant fitness model only
- Random model only
- No movement only

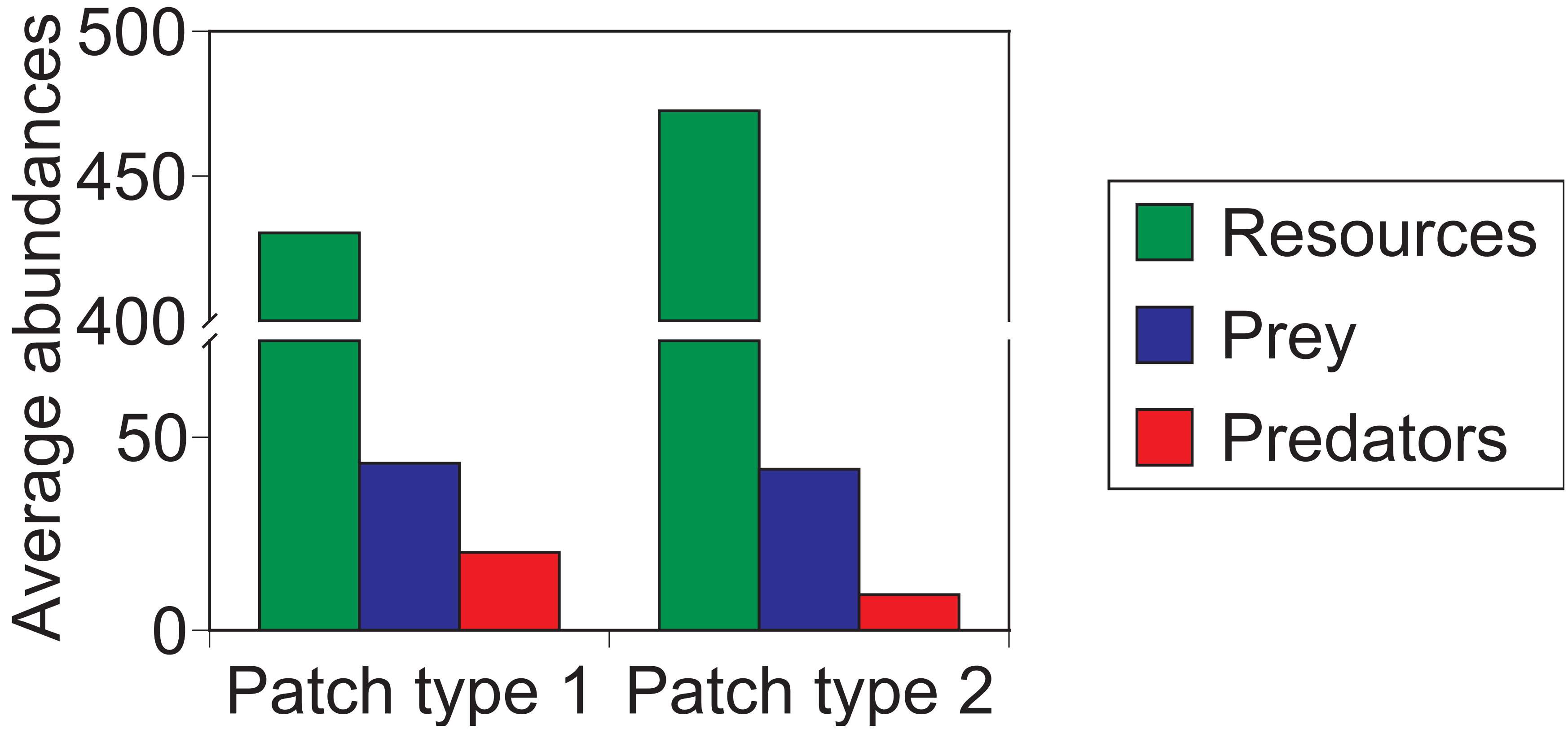
Instant fitness: Effects on probability of moving



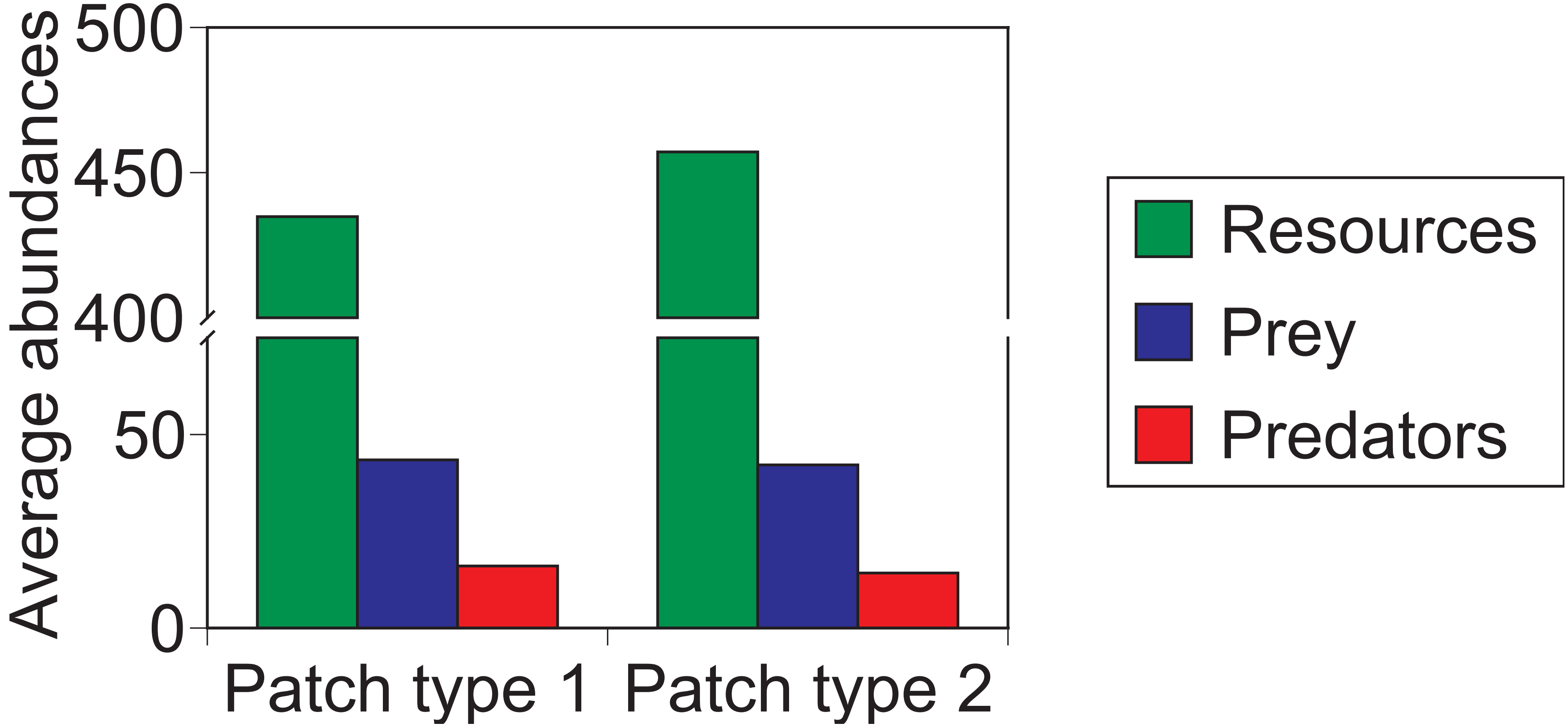
Sequential: Effects on probability of moving



Population abundances: tournament



Population abundances: fitness only

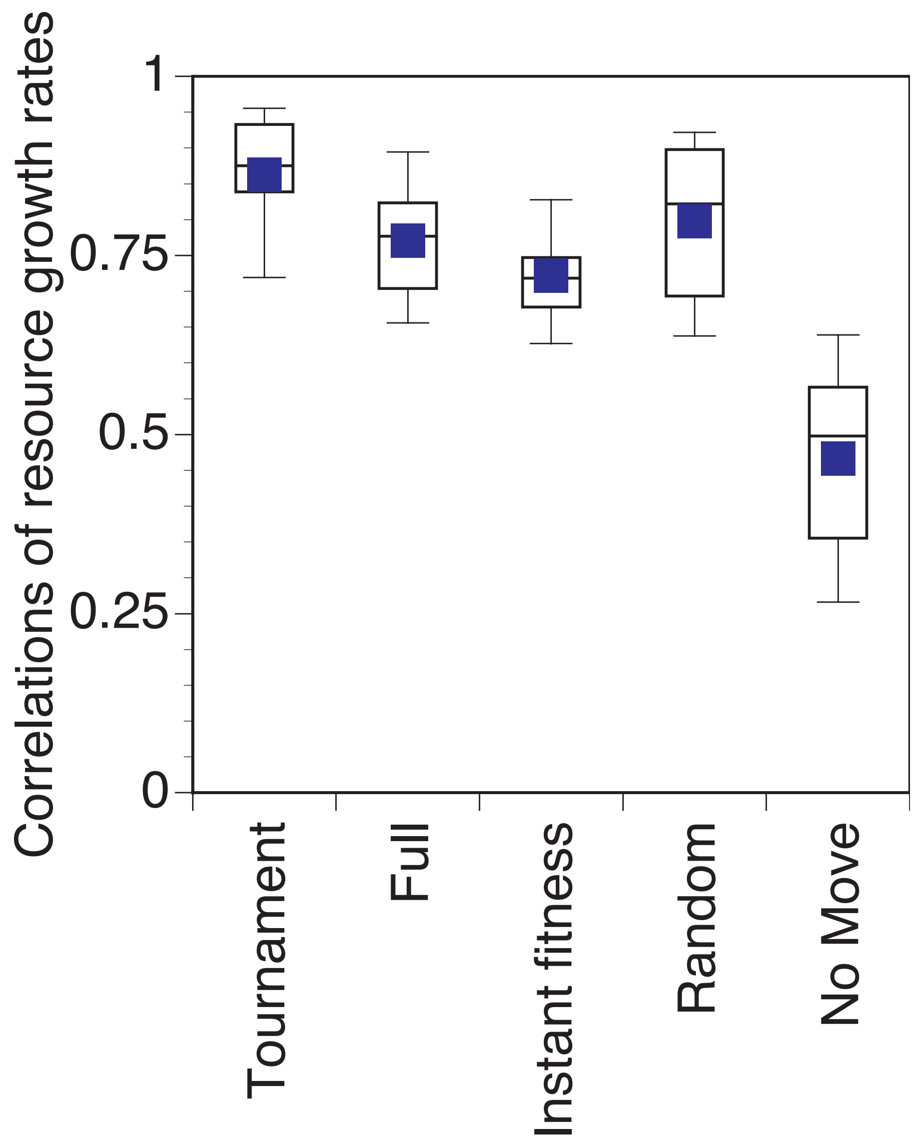


Synchronization of patches

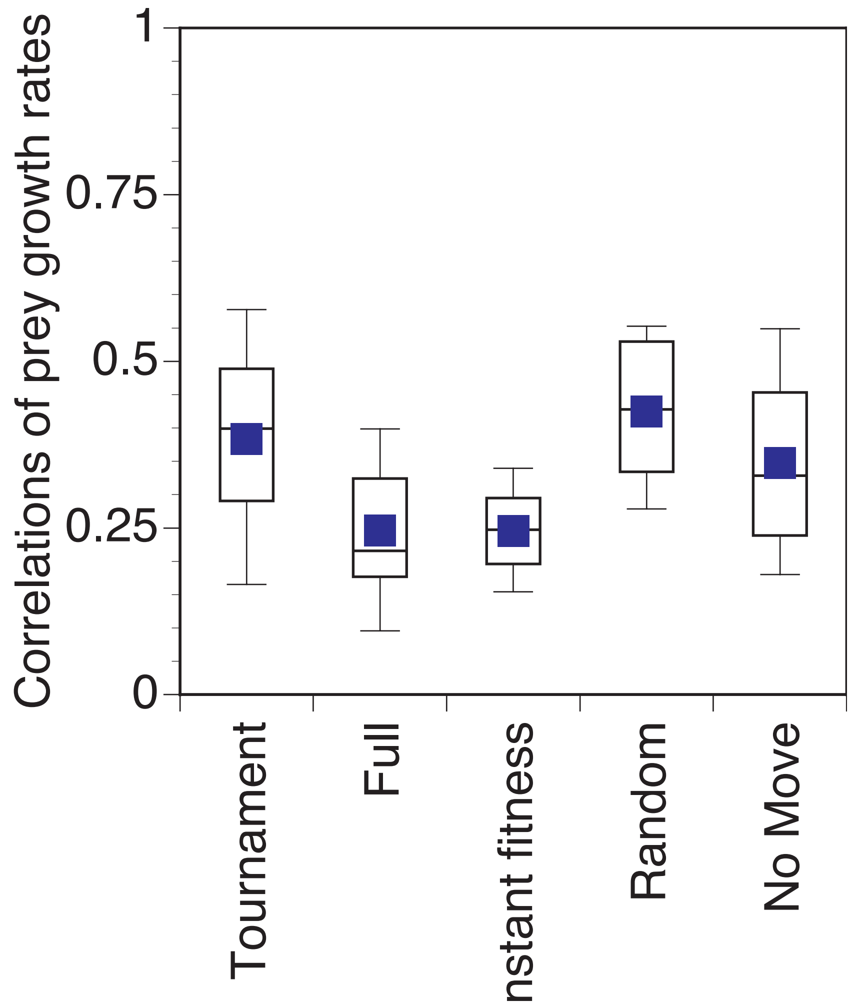
- How does movement affect the synchronization of patches (Amarasekare 2007)

- Metric: correlations in growth rates between patches, if patches are synchronized correlations will be higher

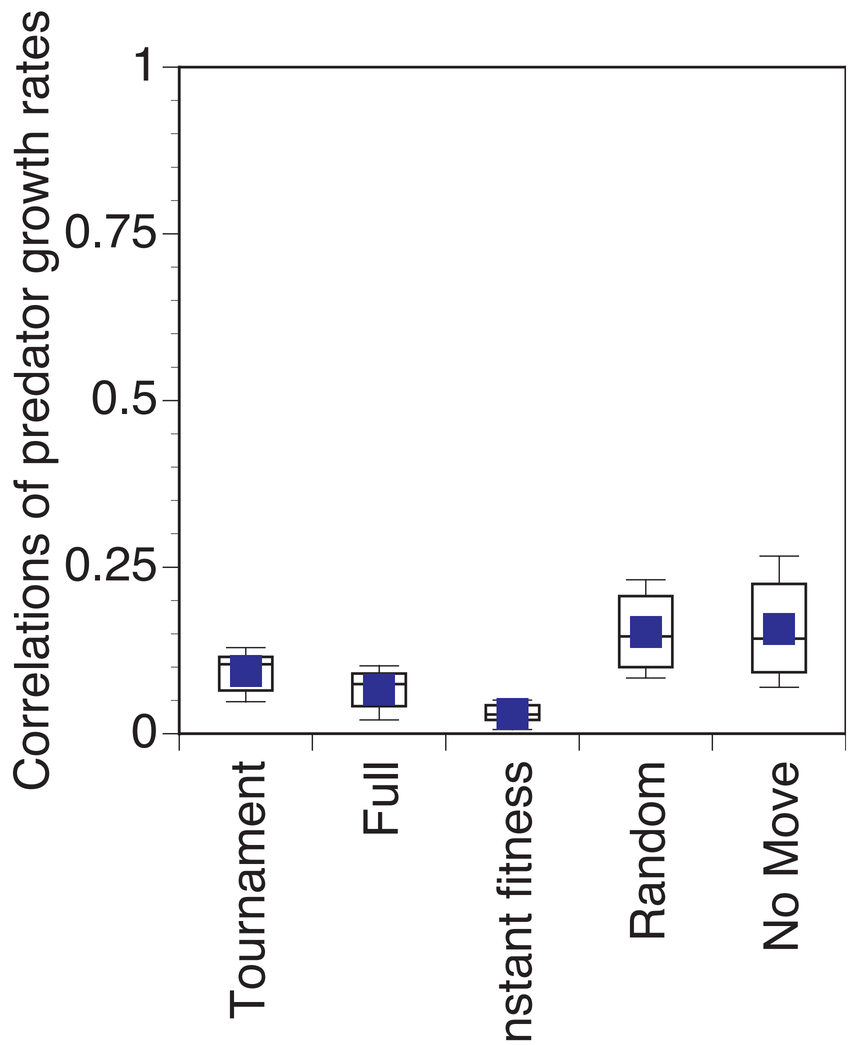
Sequential: resource synchronicity



Sequential: prey synchronicity



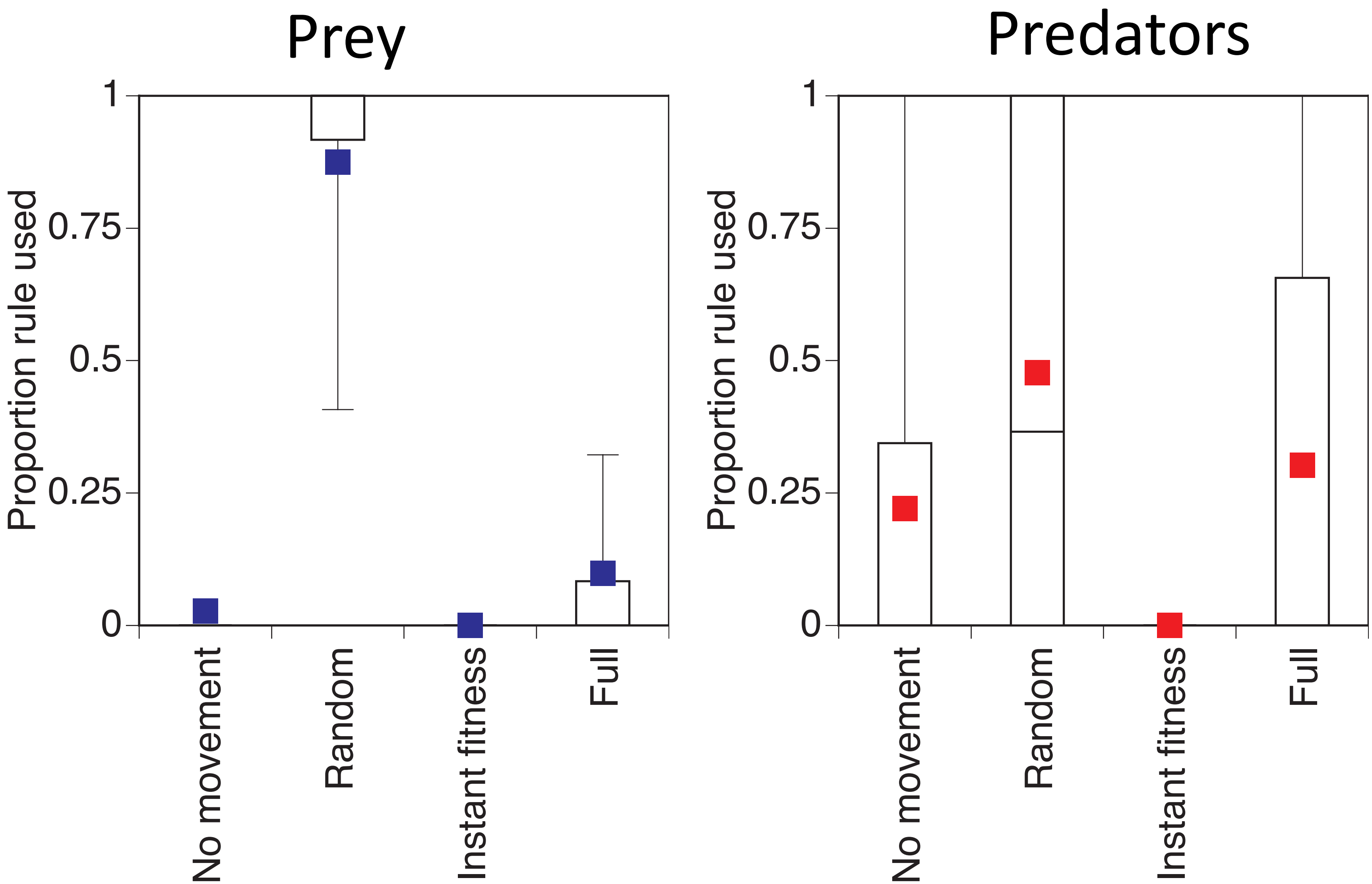
Sequential: predator synchronicity



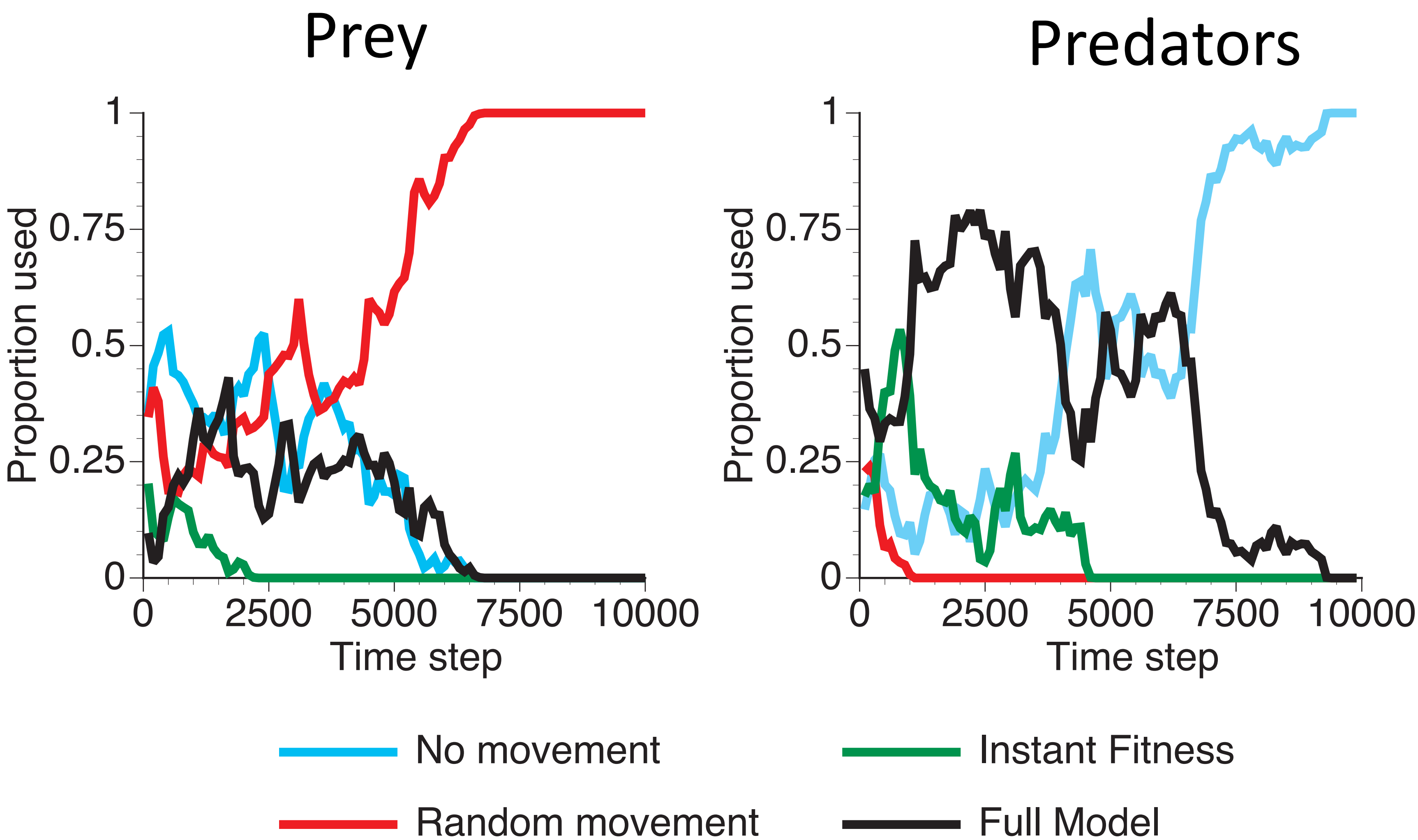
Timing of movement decisions and foraging

- Simultaneous movement
  - all simultaneously decide whether to move or stay
  - implement that decision
  - forage in random order

Simultaneous: Final rules used in Tournament

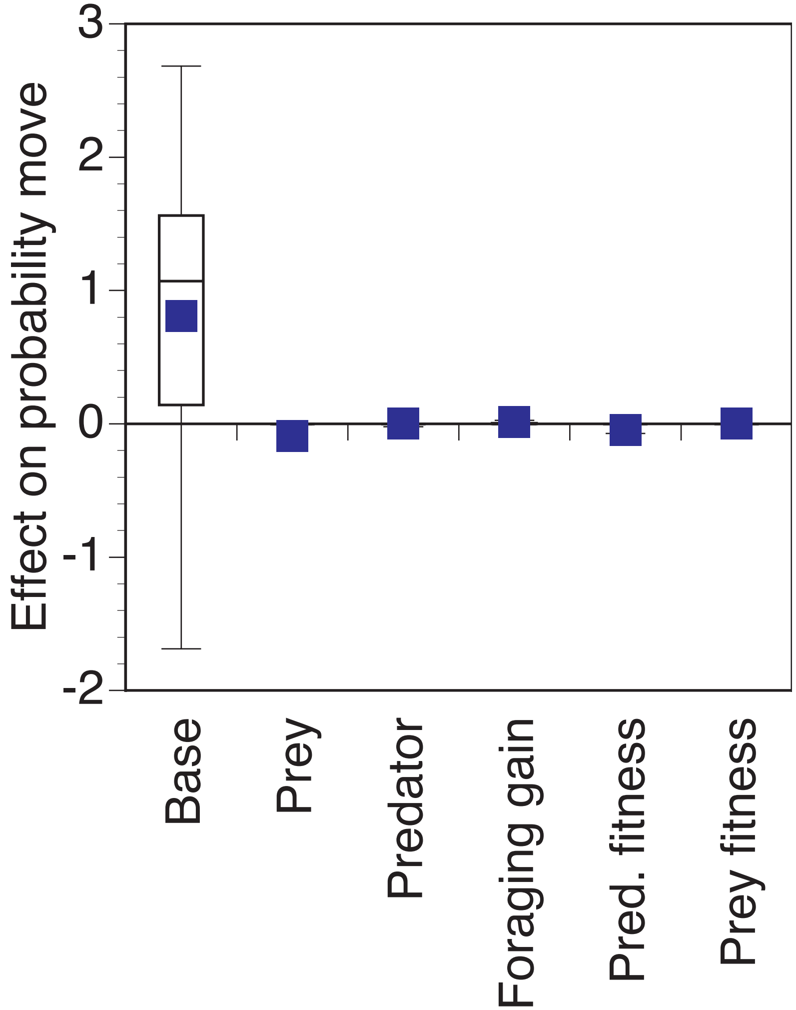


Simultaneous: Time series of rule frequencies

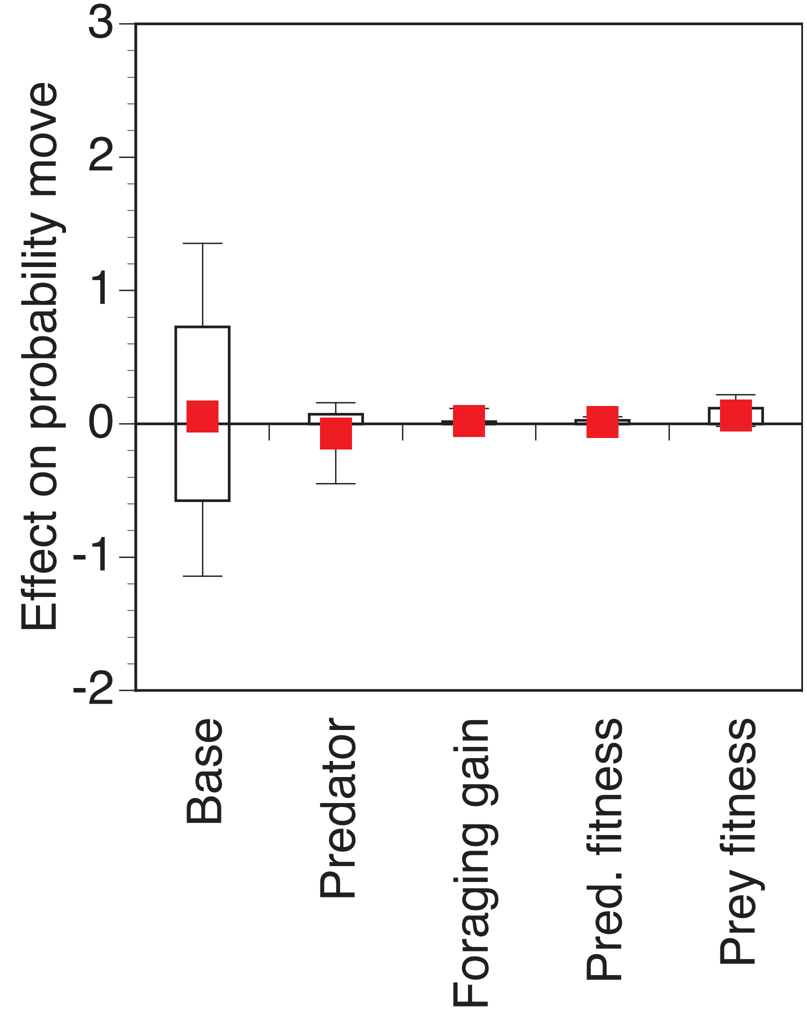


Simultaneous: Effects on probability of moving

Prey 60% move

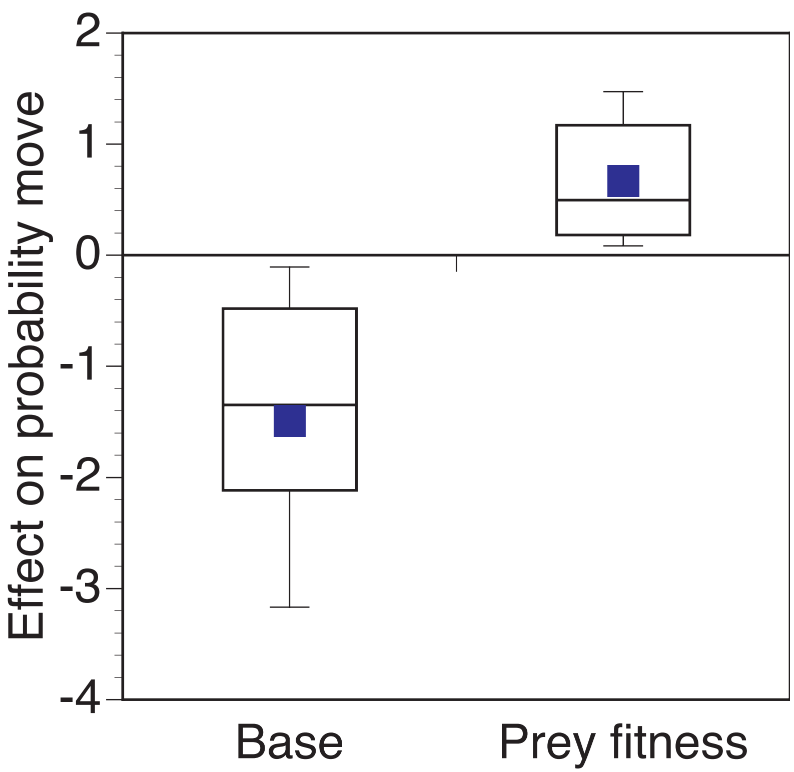


Predator 33% move

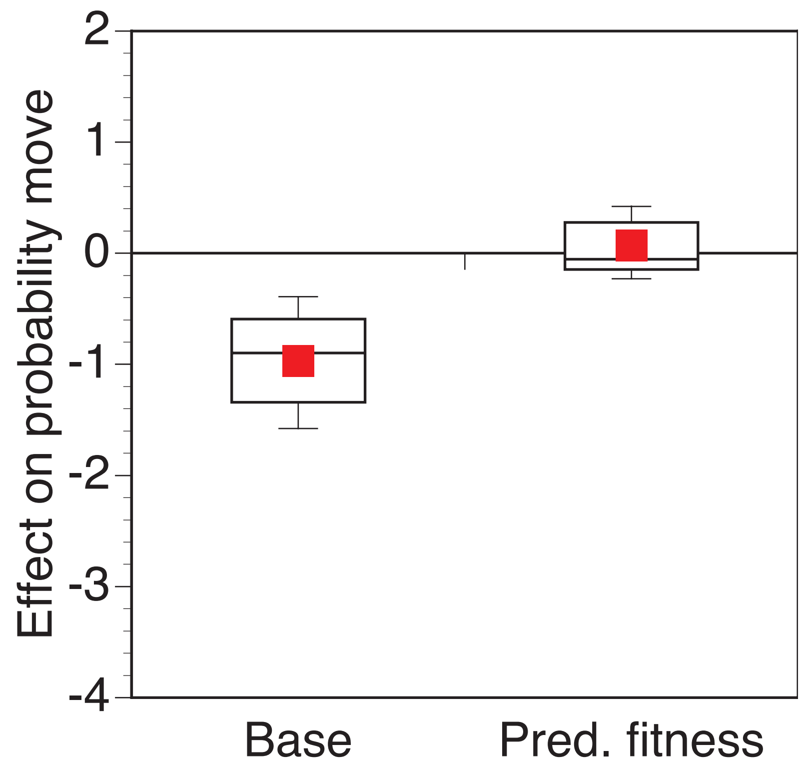


Instant fitness: Effects on probability of moving

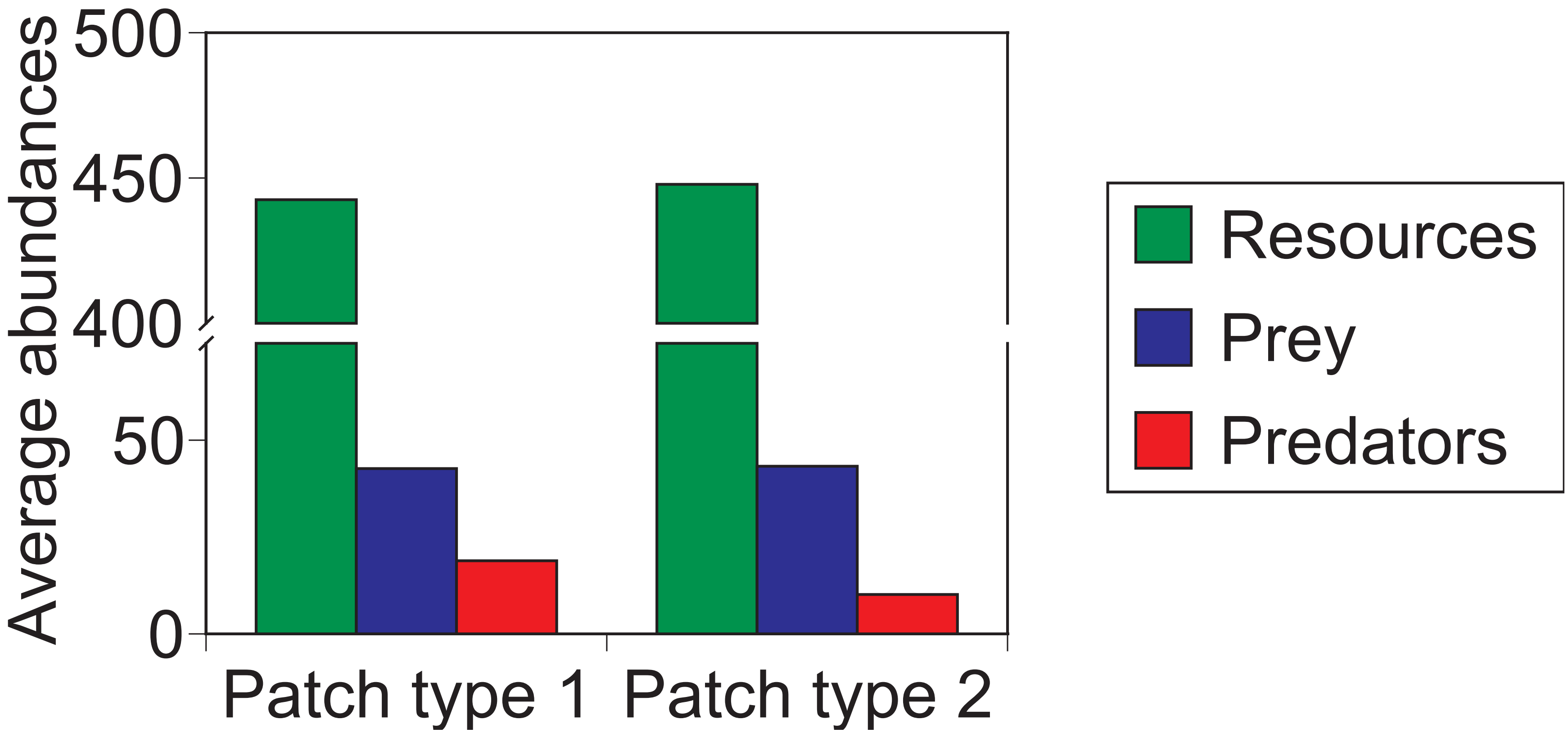
Prey 33% move



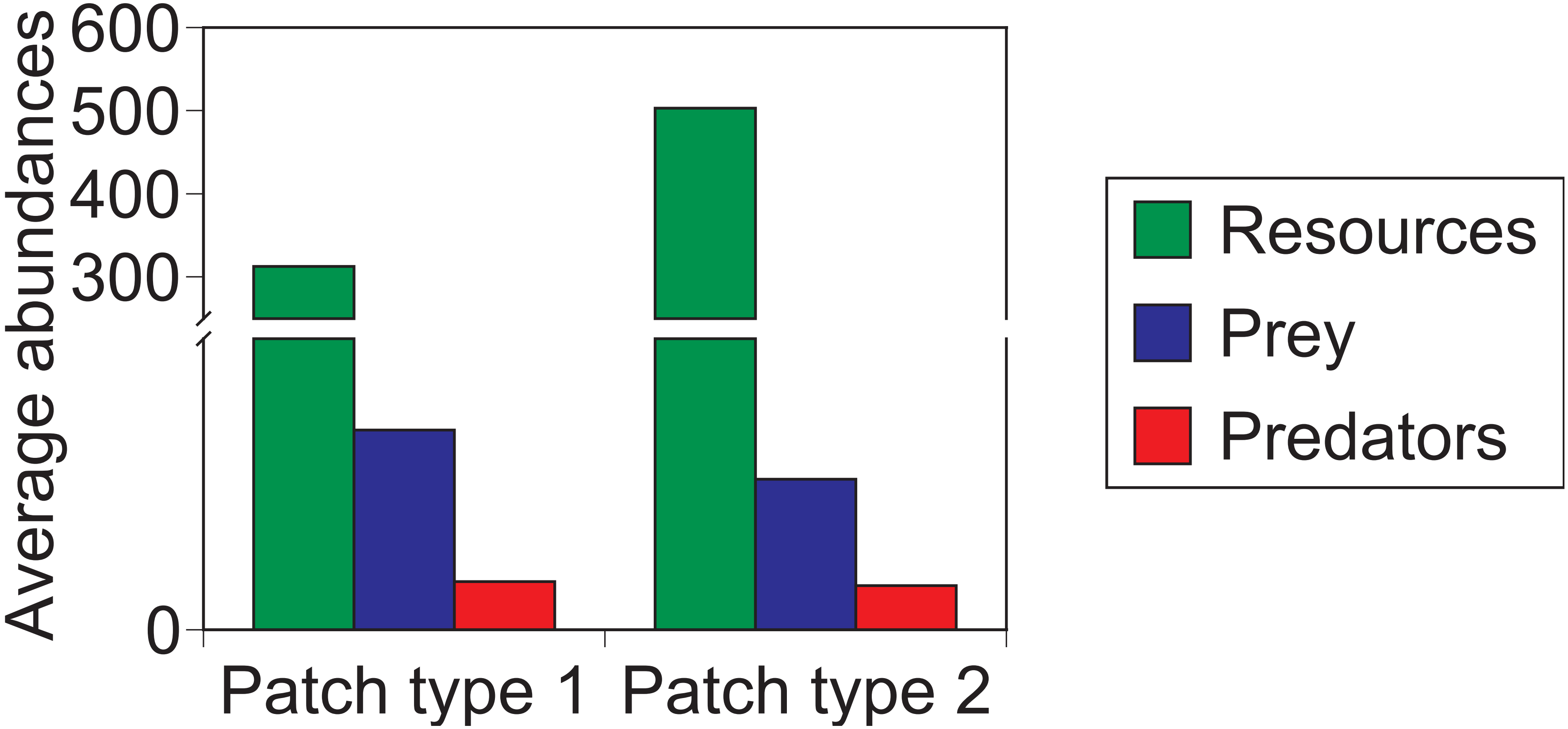
Predator 10% move



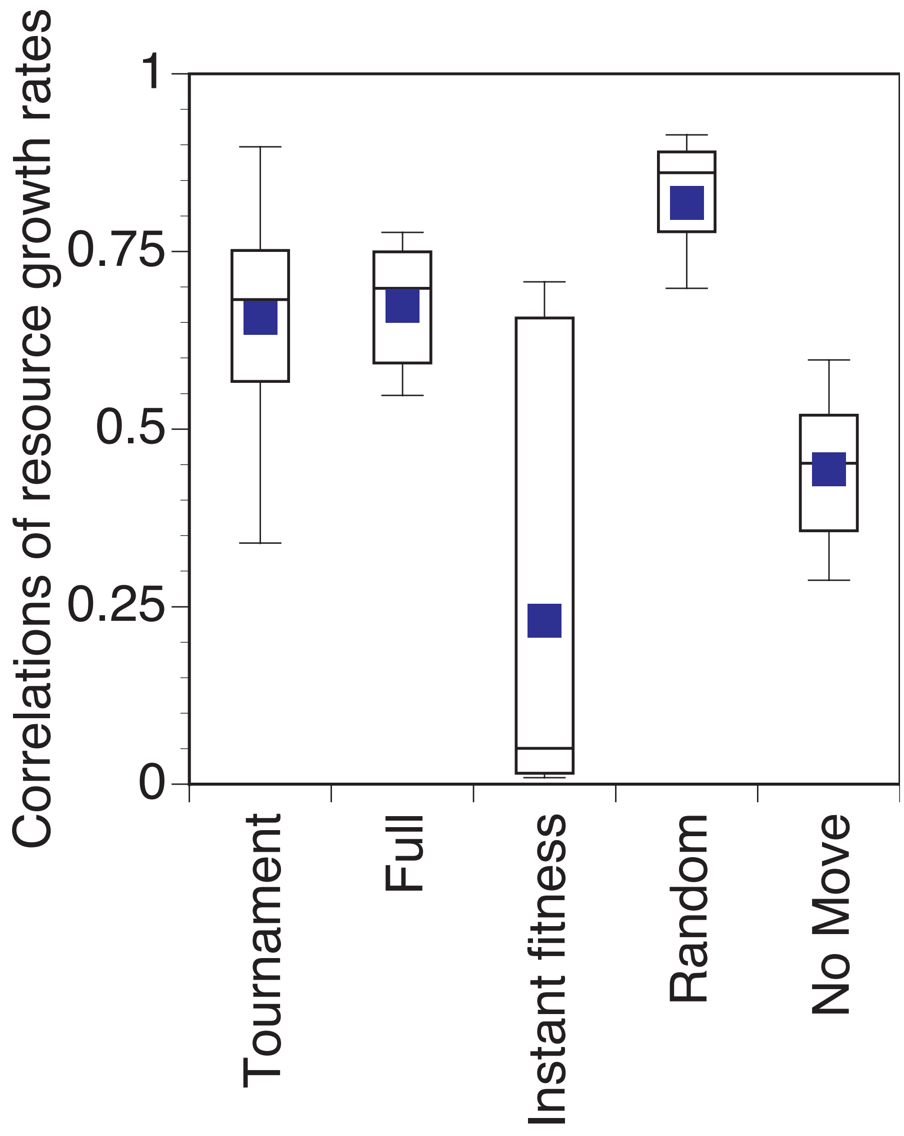
Population abundances: tournament



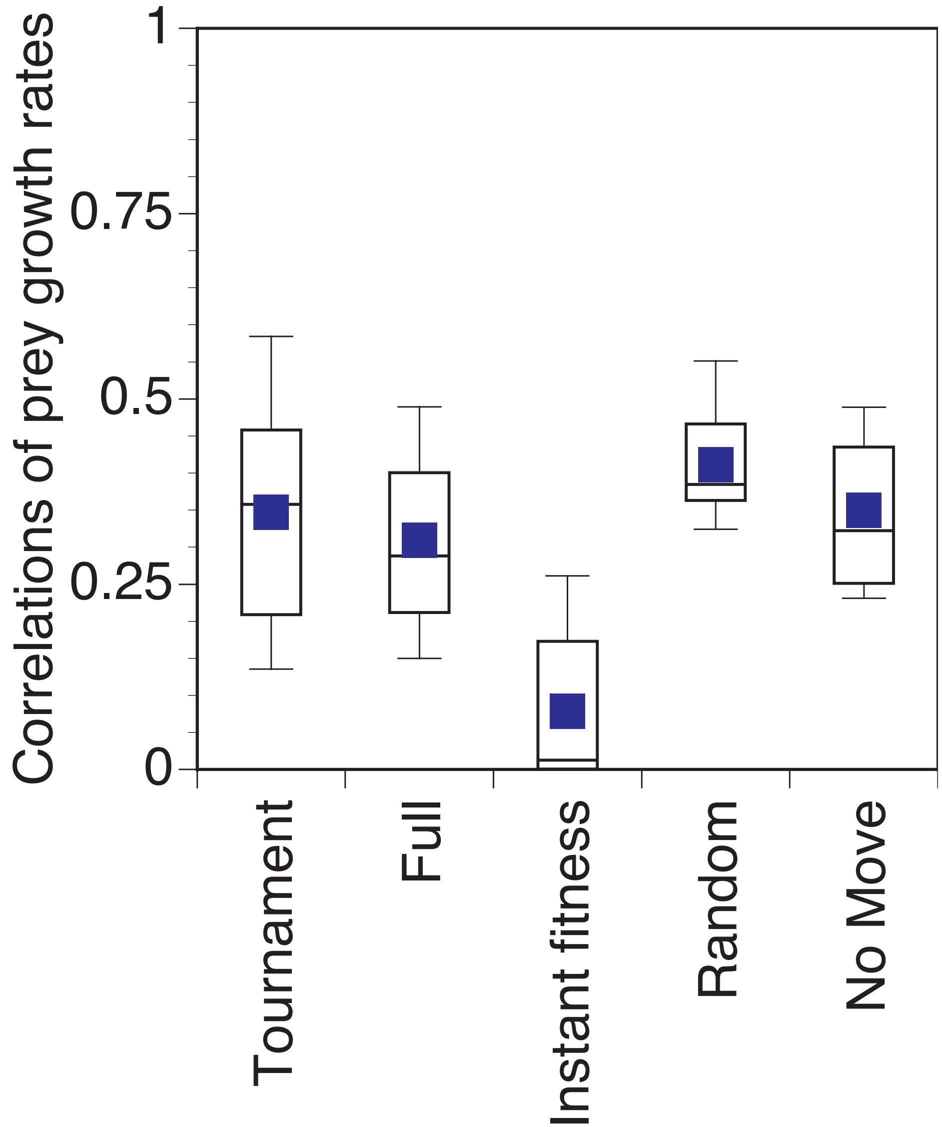
Population abundances: fit only



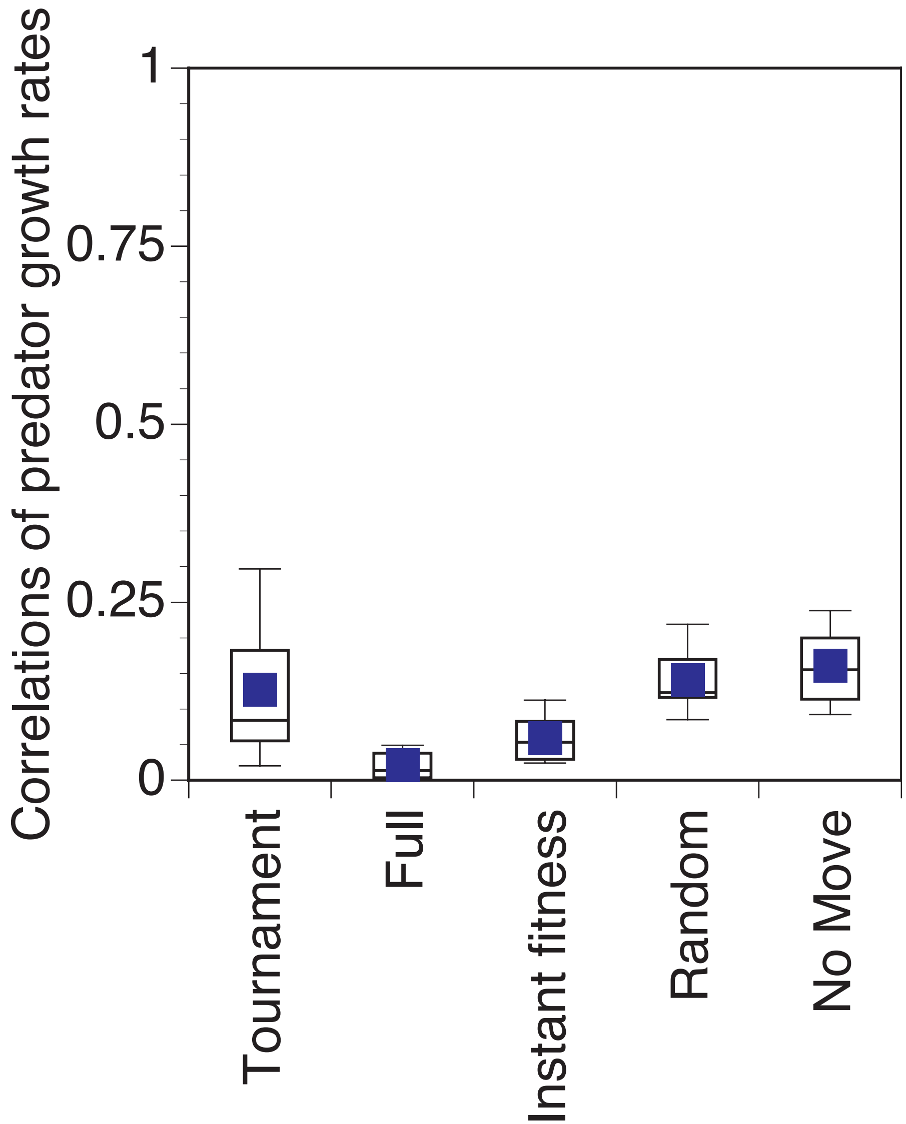
Simultaneous: resource synchronicity



Simultaneous: prey synchronicity



Simultaneous: predator synchronicity



Conclusions

- With sequential and simultaneous movement predators drive prey away from following their instant fitness
- Population abundances and synchronicity can be significantly altered by the predator and prey games that shape movement rules, but depends on the timing of movements

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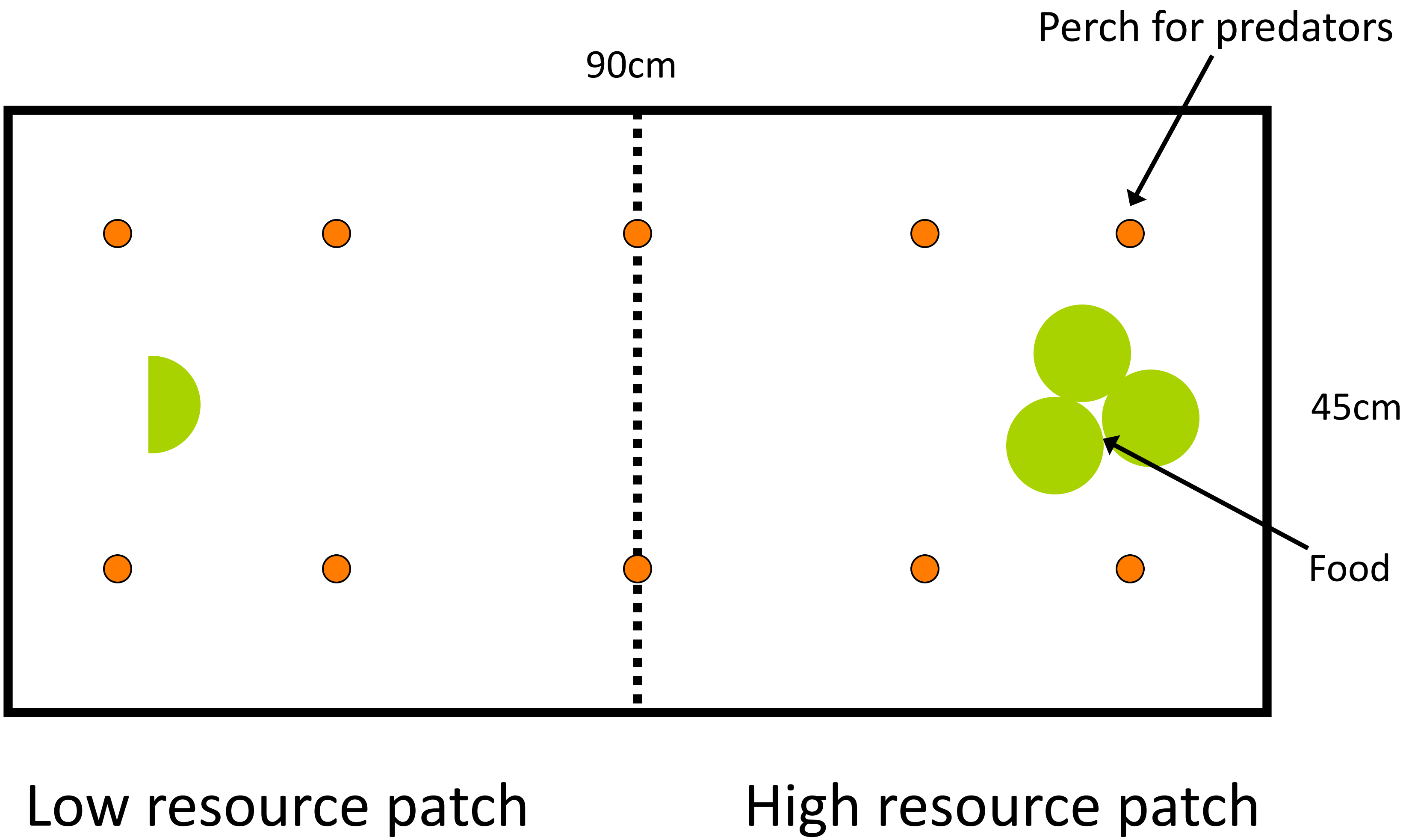
Predator-prey space game

Pacific treefrogs

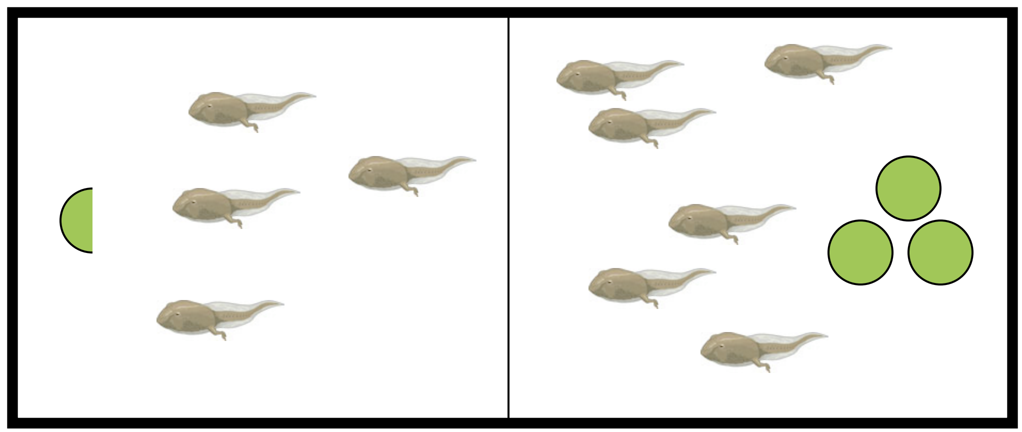
odonate predators

Collaboration with Andy Sih and John Hammond to investigate predator-prey spatial distributions

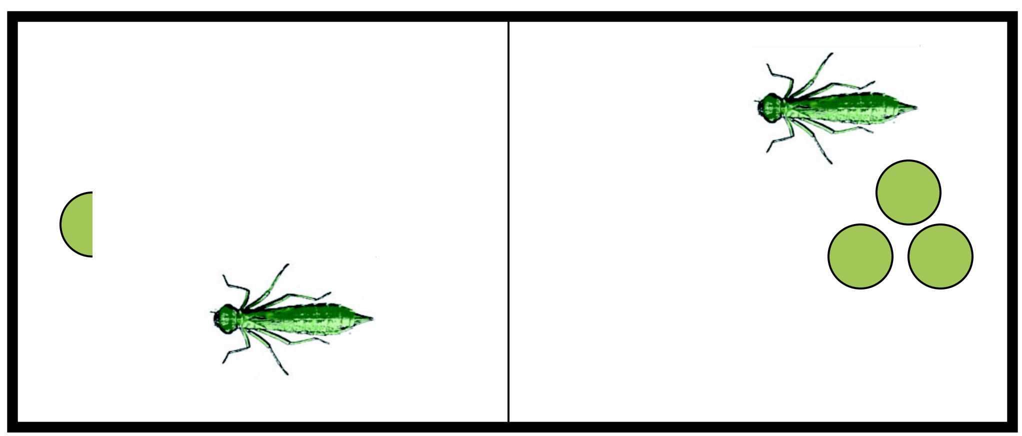
Experimental arena



Experimental protocol

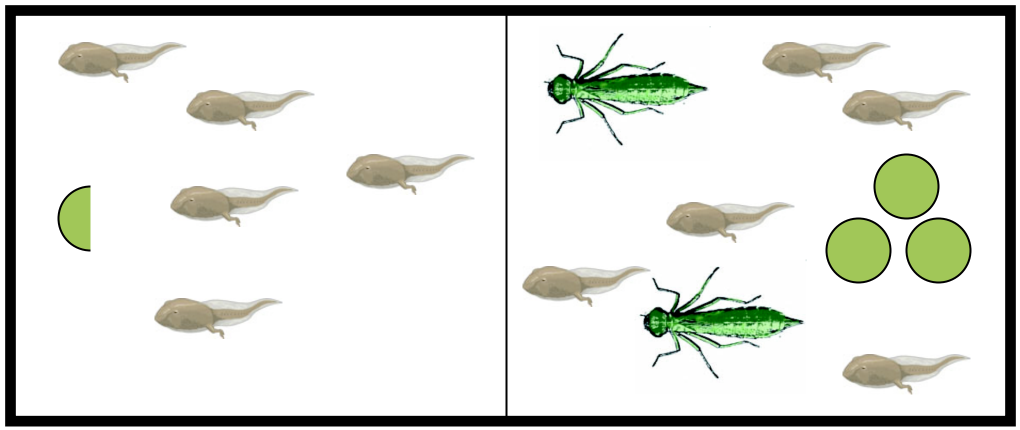


Recorded positions every 20 min for 3 hours



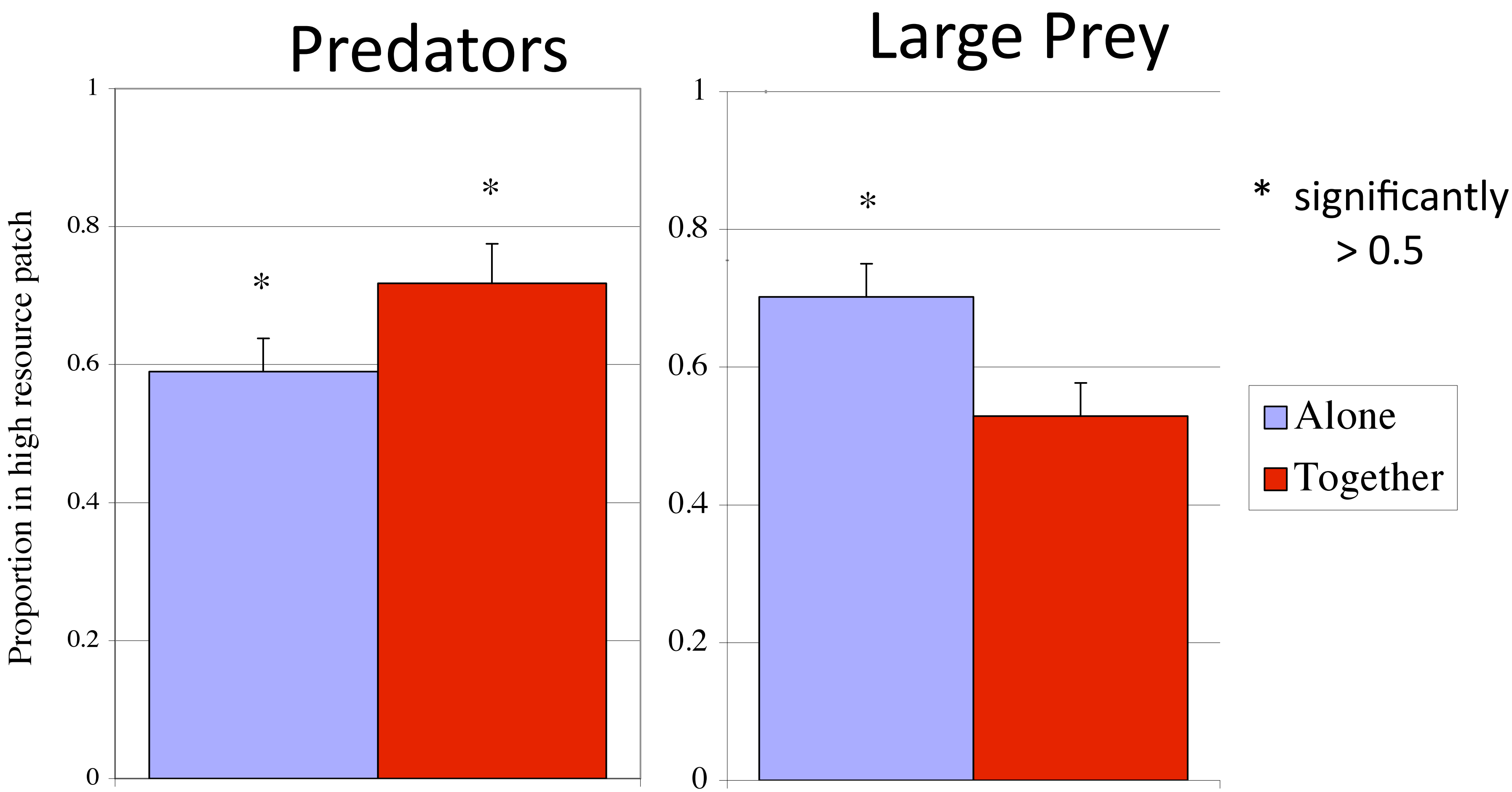
Two size classes of tadpoles used in separate trials

Experimental protocol



Recorded positions every 20 min for 3 hours

Observed patch use



Potential factors affecting predator and prey patch switching rates

- s: prey size
- r: low or high resources in patch
- n: proportion of prey in patch
- p: predators in patch

16 Alternative models for prey and for predators

$$\Pr(\text{switch patch}) = \beta_0 + \beta_s \Delta s + \beta_r \Delta r + \beta_n \Delta n + \beta_p \Delta p$$

$$\Pr(\text{switch patch}) = \beta_0 + \beta_r \Delta r + \beta_n \Delta n + \beta_p \Delta p$$

$$\Pr(\text{switch patch}) = \beta_0 + \beta_s \Delta s + \beta_n \Delta n + \beta_p \Delta p$$

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$$\Pr(\text{switch patch}) = \beta_0$$

Akaike Information Criterion

- Quantify the evidence that data give for each model
- Balances finding the best fit with using the fewest fitted parameters
- AIC = 2 L(data|model) + 2K

  K = number of fitted parameters

Prey movement models

Model				Δ AICc	Akaike weight
	r	n	p	0.0	0.68
s	r	n	p	2.1	0.24
		n	p	5.0	0.06
s		n	p	7.1	0.02
	r		p	20.7	0.00
			p	20.9	0.00
s	r		p	22.8	0.00
s			p	23.0	0.00
		n		26.2	0.00
s		n		28.2	0.00
	r	n		28.2	0.00
s	r	n		30.4	0.00
				36.1	0.00
	r			37.9	0.00
s				38.1	0.00
s	r			39.9	0.00

s - prey size
r - resources
n - prey
p - predators

Factors in prey movement

	prey size	resource	prey	predator
Summed Akaike weight	0.26	0.92	1.00	1.00
β	-0.01	-0.45	1.17	1.35

More likely to leave patches with:

- more predators
- more prey
- less resources

Predator movement models

Model	Δ AICc	Akaike weight
r p	0.0	0.37
r n p	1.5	0.17
s r p	1.9	0.14
r	2.1	0.13
s r n p	3.6	0.06
s r	4.1	0.05
r n	4.1	0.05
s r n	6.1	0.02
	11.5	0.00
s	13.0	0.00
p	13.1	0.00
n	13.4	0.00
s p	14.4	0.00
s n	14.9	0.00
n p	15.1	0.00
s n p	16.4	0.00

s - prey size

r - resources

n - prey

p - predators

Factors in predator movement

	prey size	resource	prey	predator
Summed Akaike weight	0.27	1.00	0.30	0.75
β	0.04	-1.21	0.09	0.52

More likely to leave patches with:

- less resources
- more predators

Empirical conclusions

- Predators are more abundant in patches with more of the prey’s resources
- Predators appear to cue on the abundance of the prey’s resources, more than on the abundance of the prey

Open questions

- With spatial games, climbing fitness gradients is not an optimal movement rule
- How is that altered by changes in spatial and temporal scales or opportunities to move?
- What scheduling of predator and prey moves and foraging are most appropriate?
- How are dynamics affected movement costs, imperfect information, and spatially explicit patches?