The Evolutionary Ecology of Individual Foraging Decisions

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Abstract

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Introduction

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Evolutionary Simulation Model of Individual Foraging Decisions

Our model is an individual-based evolutionary simulation whose most basic components — the environment size and shape, its gridded structure and each cell's capacity to hold multiple individuals, as well as the discrete conception of time within and between generations — is taken from Netz et al. *in prep.*. We conceptualised the model and the scenarios around the behaviour of waders (*Charadrii*, and especially oystercatchers *Haematopus sp.*), which are extensively studied in an optimal foraging context (e.g. Ens et al., 1990; Vahl et al., 2005*a,b,c*). We simulated a fixed population with a fixed size of 10,000 individuals moving on a landscape of 512^2 grid cells, with the landscape wrapped at the boundaries so that individuals passing beyond the bounds at one end re-appear on the diametrically opposite side. Individuals have a lifetime of T timesteps, with T set to 400 by default. After their lifetime, individuals reproduce and transmit their heritable traits proportional to their fitness over their lifetime. The model code (in C++) can be found as part of the Supplementary Material in the Zenodo repository at **Zenodo/other repository here**.

Flexibility in Foraging Strategies

Our model considers three main scenarios of flexibility in individual foraging strategies. The **first scenario** is an inflexible producer-only case, in which individuals move about on the landscape and probabilistically find and consume discrete prey food items. Between finding and consuming a food item, individuals must 'handle' the prey for a fixed handling time T_H which is constant across prey items. Prey handling time T_H is set at 5 timesteps by default. The handling time dynamic is well known from many systems; for instance, it could be the time required for a wader to break through a mussel shell, with the handling action obvious to nearby individuals,

26 and the prey not fully under the control of the finder. We refer to such individuals as 'handlers'

27 for convenience. Handlers are assumed to be fully absorbed in their processing of prey, and do

28 not make any movements until they have fully handled and consumed their prey. The **second**

29 **scenario** is a fixed-strategy case which adds some flexibility. Individuals at the start of their

30 lifetime each choose between two foraging strategies, which are then fixed through life. The

31 strategy choice is based on local environmental cues, and is covered in "Movement and Foraging

32 Decisions". The two strategies are to produce, i.e., to probabilistically find, handle, and consume

33 discrete prey (as in the producer-only case), or to scrounge as a kleptoparasite, i.e., to steal a

34 found prey item from the individual handling it. We refer to such scroungers as 'kleptoparasites'

35 from here onwards. Kleptoparasites can steal from any handler, regardless of whether that

36 handler acquired its prey by searching or theft. Kleptoparasites are always successful in stealing

37 from the handler they target; this may be thought of as the benefit of the element of surprise, a

38 common observation in nature. Having acquired prey, a kleptoparasite need only handle it for

39 $T_H - t_h$ timesteps, where t_h is the time that the prey has already been handled by its previous

40 handler. The targeted handler deprived of its prey is assumed to flee from the area, and does not

41 make a further movement decision. Thus kleptoparasites clearly save time on handling compared

42 to a producer, and the time saved increases with the handling time T_H of the prey. The **third**

43 **scenario** is a flexible-strategy case, and individuals are allowed to be plastic in their foraging

44 strategies, and choose between producing and scrounging strategies in each timestep. Apart

45 from the frequency of the choice, the actual foraging dynamics are the same as described in

46 the fixed-strategy case. Individuals move about on the environment, and each foraging strategy

47 choice is based on local environmental cues (see "Movement and Foraging Decisions").

Movement and Foraging Decisions

49 Individuals essentially use cues available in timestep t to predict their best move for the next

50 timestep $t + 1$, and the strategy associated with that move (when this is allowed). The movement

51 decision is based on three local environmental cues: (1) the number of discrete prey items G,

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52 (2) the number of individuals handling prey H (referred to as 'handlers'), and (3) the number of

53 individuals not handling prey P (referred to as 'non-handlers'). The notation is chosen in keeping

54 with Netz et al. *in prep..* These cues are available to individuals in all three model scenarios.

55 Individuals occupy a single grid cell on the environment at a time, and assign a suitability score

56 S incorporating G, H, and P per cell to the nine cells in their Moore neighbourhood (including

57 their current cell). Following Netz et al. *in prep.*, individuals calculate the cell-specific S as

$$S = m_g G + m_h H + m_p P + m_b$$

59 where the weighing factors for each cue m_g, m_h and m_p, and the bias m_b are genetically encoded

60 and heritable between generations. Individuals rank their Moore neighbourhood by S in timestep

61 t and move to the highest ranked cell in timestep $t + 1$.

62 Individuals in the producers-only case make no foraging decisions and find food items prob-

63 abilistically (see "Prey Environment and Ecological Dynamics"). In the fixed-strategy case, indi-

64 viduals pick a lifelong foraging strategy in their first timestep (t_0), while in the flexible-strategy

65 case, individuals pick a strategy in each timestep t to be deployed in $t + 1$. Individuals in these

66 latter two cases process the cell-specific environmental cues G, H, and P to determine their for-

67 aging strategy F for life (fixed strategy), or in the grid cell into which they have chosen to move

68 in $t + 1$ (flexible strategy). F is determined as

$$F = \begin{cases} producer, & \text{if } f_g G + f_h H + f_p P + f_b \geq 0 \\ scrounger, & \text{otherwise} \end{cases}$$

70 where the cue weights f_g, f_h and f_p, and the bias f_b are also genetically encoded and heritable

71 between generations.

72 In both latter cases that allow for kleptoparasitism, individuals make their foraging strategy

73 choice for the next timestep after they have passed through the ecological dynamics of their cur-

74 rent location. This excludes individuals that have been stolen from are an important exception;

75 these fleeing agents are moved to a random cell within a Chebyshev distance of 5, and do not

76 make a foraging decision there. Thus kleptoparasitism not only gains individuals prey items

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77 while depriving the targeted individual, it also displaces a potential competitor. All individu-

78 als move simultaneously, and attempt to implement the foraging strategy chosen for their new

79 location (see below).

Prey Environment and Ecological Dynamics

81 Since our model was initially conceived to represent foraging waders, we developed a resource

82 landscape based on mussels (family *Mytilidae*) that are commonly found in inter-tidal systems.

83 Mussels beds share some important characteristics with other discrete prey items. Firstly, mussels

84 are immobile relative to their consumers, and their abundances are largely driven by extrinsic

85 environmental gradients and very small-scale interactions (de Jager et al., 2020, 2011). Secondly,

86 in common with many ecological systems (Levin, 1992), mussels are not uniformly distributed

87 across the inter-tidal mudflats, and are instead strongly spatially patterned into clusters ('beds')

88 (de Jager et al., 2020, 2011). Thirdly, while prey or their signs in an area are often visible to

89 consumers, consumers are not always certain of obtaining one of these prey, since prey can show

90 small-scale anti-predator avoidance responses.

91   We captured these essential aspects of prey dynamics when implementing the resource land-

92 scape on which our individuals move. We modelled relative prey immobility and extrinsically

93 driven abundance by assigning each grid cell of the resource landscape a constant probability of

94 generating a new prey item per timestep, which we refer to as the growth rate r. We modelled

95 clustering in the abundance of prey by having the distribution of r across the grid cells take the

96 form of 1,024 uniformly distributed resource peaks with r declining from the centre of each peak

97 to its periphery (Figure X). Effectively, the cell at the centre of each patch generates a prey item

98 five times more frequently than the cells at the edges. Thus for a simulation-specific baseline r_{base}

99 = 0.03, the central cell of a resource peak would have an $r_{centre} = 0.03$, and generate 3 items every

100 100 timesteps, compared with $r_{edge} = 0.006$, or 0.6 items generated in 100 timesteps. We ran

101 the simulation with r_{base} values of 0.001, 0.01, 0.03, and 0.05, which we considered a sufficiently

102 broad range. Cells in our landscape were modelled as being able to hold a maximum of K prey

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items, with the default $K = 5$. While a cell is at carrying capacity its r is 0. We modelled near-perfect intermediate-range perception but uncertain short-range acquisition of prey by allowing individuals to perceive all prey items G in a cell, but giving individuals which choose a producer strategy only a probability of finding one of these prey. The probability of finding a prey item $p(success)$ is given as the probability of not finding any of G prey

$$p(success) = 1 - (1 - p_i)^G$$

where p_i is the detection probability of each of G items, which is uniformly set to 0.2 by default for all items.

Since we model foraging events as occurring simultaneously, it is possible for more producers to be considered successful in finding prey than there are discrete items in that cell. We resolve this simple case of exploitation competition by assigning G prey among some N successful finders at random. Producers that are assigned a prey item in timestep t begin handling it, and are considered to be handlers for the purposes of timestep $t + 1$ (primarily movement and foraging decisions of other individuals). It is important to note that a producer that has converted into a handler in timestep t is not an available target for kleptoparasites until timestep $t + 1$. Producers that are not assigned a prey item are considered idle during timestep t, and are counted as non-handlers for $t + 1$.

Kleptoparasites in the fixed- or flexible-strategy case face a slightly different challenge. All kleptoparasites in a cell successfully steal from a handler, contingent on the number of handlers matching or exceeding the number of kleptoparasites in timestep t. When the number of kleptoparasites exceeds handlers, handlers are assigned among kleptoparasites at random. Successful kleptoparasites convert into handlers, and similar to producer-handlers are unavailable as targets to other kleptoparasites until the next timestep. Unsuccessful kleptoparasites are considered idle, and are also counted as non-handlers for timestep $t + 1$. A handler that finishes processing its prey in timestep t returns to the non-handler state and is assessed as such by other agents when determining movements for $t + 1$.

129   Individuals move and forage on the resource landscape for T timesteps per generation, and

130   T is set at 400 by default. Handling a food item requires a maximum of T_H timesteps, during

131   which the handler is immobile.

Reproduction and the Evolution of Decision Making

133   At the end of each generation, the population is replaced by its offspring, maintaining the fixed

134   population size, and the decision-making weights which determine individual movement (m_g,

135   m_h, m_p, m_b) and foraging strategy choice (f_g, f_h, f_p, f_b) are transmitted from parent individuals

136   to offspring. The number of offspring of each parent is proportional to the parent's share of the

137   population fitness, and this is implemented as a weighted lottery that selects a parent for each

138   offspring. The total lifetime intake of individuals is used as a proxy of fitness, and the popu-

139   lation's total fitness is its total intake. The decision-making weights are subject to independent

140   random mutations with a probability of 0.001. The size of the mutation (either positive or nega-

141   tive) is drawn from a Cauchy distribution with a scale of 0.01 centred on the current value of the

142   weight to be mutated. This allows for a small number of very large mutations while the majority

143   of mutations are small. Autocorrelation in the landscape coupled with limited natal dispersal

144   can lead to spatial heterogeneity becoming fixed in populations, as lineages adapt to local con-

145   ditions. Among other things, this could lead to population-level movements due to differential

146   reproduction that mirror shifts in resource abundance, rather than individual movement. To en-

147   sure individual movement rules evolved, we intialised each offspring at a random location on

148   the landscape, and also reset its total intake to zero.

Simulation Output and Analysis

150   *Spatial Distribution of Individuals, their Intake, and Prey Items.*   Over each of the last eight gen-

151   erations of the simulation (991 − 998), we summed the following for each grid cell ij over the

152   generation's timesteps: (1) the number of prey items G, (2) the number of individuals following

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each of the two strategies, producer N_p or kleptoparasitic scrounger N_s, and (3) the intake (in food items consumed after handling) by agents following each of the two strategies, producer I_p or kleptoparasite I_s. For instance, the number of producer individuals in a generation to inhabit a cell ij would be

$$N_p = \sum_{t=0}^{i=T} n_{p_t}$$

where $t \in (0, 1 \ldots T = 400)$, and n_{p_t} is the number of producers in cell ij at each timestep t. We saved this generation- and simulation- specific data to file, and these data are available at the Zenodo/IRODS repository at **Zenodo/other link here**. The volume of data at this stage was comparable to a very high-resolution, long-term ecological study, and we handled it accordingly. First, we processed the data to get the timestep-averaged values of G, N_p, N_s, I_p, and I_s for each cell, dividing each value by T (400). From this data, we calculated the per-capita intake rate (I per t) on each cell for each of the two strategies separately, which we denote as R_p (producers) and R_s (scroungers). We plotted the timestep- and generation-averaged item count (G), strategy count (N_p, N_s), and absolute and per-capita intake (I_p, I_s, and R_p, R_s) in relation to grid-cell quality (the growth rate, r) to investigate the spatial distribution of individuals (see Figure X).

Generalised Functional Response. In our simulation, individuals perceive and respond to the standing stock of prey items G on a cell rather than its growth rate r. This standing stock is unpredictable due to consumption by other individuals. To understand the consequences of movement, we need to investigate how individual intake rate varies with G as well as the presence of potential competitors. Thus we examined the generalised functional response (W) *sensu* Meer and Ens (1997). We plotted the per-capita intake rate achieved by individuals on grid-cells with similar numbers of prey items (G) and individuals ($N_p + N_s$) (see Figure Xa). We did this separately for W_p and W_s, the generalised functional response of individuals using the producer and kleptoparasitic scrounger respectively (see Figure Xb, Xc). We modelled the effect of competition and resource availability on W_p and W_s using a simple generalised linear model (GLM) with either W_p or W_s as the response, and the number of individuals and the number

of prey items as the only additive predictors. We repeated this for simulations with different baseline growth rates r, and examined variation in the contribution of competition and resource availability in the **form of the linear model coefficients of individual density and item density, respectively (see Figure X)**. These linear models took the form

$$W = \beta_0 + \beta_1 G + \beta_2 (N_p + N_s)$$

where W is either W_p or W_s. We fit these models for each r_{base} separately, but did not distinguish between replicates.

Decision Making Weights. To understand the evolutionary consequences of our simulation, we exported the the decision-making weights which determine individual movement (m_g, m_h, m_p, m_b) and foraging strategy choice (f_g, f_h, f_p, f_b) of each individual in every generation of the simulation. We examined how the frequency of these weights changed over the simulation, i.e., how the weights evolved. We visualised weights' evolution after scaling them between -1 and +1 using a hyperbolic tangent function, and binning the scaled values into intervals of 0.1. We refer to these scaled and binned values as phenotypes for convenience. Weights at or near -1 would represent the maximum evolved avoidance of an environmental cue (in relation to a movement weight) or the greatest evolved negative effect of a cue on choosing the foraging strategy (in relation to a strategy choice weight). Similarly, weights at or near +1 represent the greatest evovled preference for or positive effect of a cue on the movement and strategy choice mechanism of an individual.

Simulation Model Outcomes

Emergence of a Dynamic Equilibrium

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Evolution of Movement Decisions

Response to Prey Items.   Populations across scenarios consistently evolved to move towards food items, with all individuals evolving positive values of m_g across regrowth rates (Fig. 1.a). However, across scenarios, replicates and growth rates, populations did not converge upon a single value of m_g, with a similar number of phenotypes evolved across replicates (Fig. 1.e). Scenarios 2 and 3 showed opposite relationships between the number of m_g phenotypes and r_{base}: in scenario 2, there were only about half as many phenotypes as in scenario 3 for $r_{base} \leq 0.1$, while at the highest r_{base} (0.25), there were almost four times as many phenotypes in scenario 2 as in scenario 3.

Response to Handling Individuals.   Populations across scenarios evolved to move towards handling individuals at low growth rates, with most individuals in the final generation having positive values of m_h ($r_{base} < 0.05$; Fig. 1.b). At higher growth rates, populations in scenario 3 consistently evolved a preference for handling individuals, with variation in the number of phenotypes declining with increasing r_{base}(Fig. 1.b, f). In scenarios 1 and 2 however, the proportion of the population with an evolved preference for moving towards handling individuals declined at higher growth rates, with only between 25% and 50% of the population showing such a preference at the highest growth rate. This decreasing preference for handlers was accompanied by an increase in the number of negative phenotypes of m_h, though the number of positive phenotypes was maintained despite the lower proportion of individuals with a positive m_h.

Response to Non-Handling Individuals.   Acros scenarios, populations evolved to move away from non-handling individuals when growth rates were low, with most individuals in the final generation having negative values of m_p ($r_{base} < 0.1$; Fig. 1.c). At higher growth rates, however, populations in scenarios 1 and 2 evolved no particular preference or avoidance of non-handlers, while in scenario 3 the population consistently evolved to move towards non-handling individuals. There was wide variation in the strength of avoidance (and at higher r_{base}, preference), with

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multiple m_p phenotypes (Fig. 1.g).

Overall Response to Individuals. On summing, transforming, and binning the weights for handling and non-handling individuals, the evolved preferences for individuals in total were distinct to each scenario. Populations in scenario 3 evolved a consistent preference for moving towards individuals overall (Fig. 1.d).In scenario 2, the proportion of the population with an overall preference for moving towards individuals declined linearly with growth rate. At the two highest growth rates (0.1, 0.25), about 50% of fixed-strategy individuals preferred to move towards other individuals. Scenario 1 showed a strongly non-linear, inverse hump-shaped relationship between the preference for individuals and growth rates. At very low growth rates ($r_{base} \approx 0.001$), about half the population had an overall preference for moving towards other individuals. This proportion declined until nearly all individuals avoided each other when choosing where to move for $0.01 \geq r_{base} < 0.1$. Across high growth rates (≥ 0.1), an increasing proportion of individuals preferred to move towards other individuals overall (Fig. 2.d).

Evolution of Foraging Strategy

Populations in scenario 3 were fixed to choose a producer strategy, and their foraging strategy weights evolved neutrally, providing a null model of weight evolution against which to compare scenarios 2 and 3. Populations in scenario 3 did not show a consistently evolved bias towards choosing a producing strategy, with no discernible pattern in the proportion of the population bearing a positive f_b (Fig. 2. a). However, populations in scenario 2 showed an increasing proportion of individuals biased towards a foraging strategy with increasing r_{base}. At the highest growth rate, all evolved individuals in scenario 3 were biased towards producing (Fig. 2.a).

Populations across scenarios, growth rates, and replicates evolved to seemingly ignore prey items and non-handling individuals when making a foraging decision, with no consistency in the proportion of individuals bearing positive f_g and f_p across replicates of the same scenario and growth rate(Fig. 2.b,d). Howevever, evolved populations in scenario 3 were more likely to

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uniformly choose a foraging strategy based on the number of non-handling individuals, with more variation within rather than between growth rates.

The number of handling individuals was not processed similarly by individuals evolved in scenario 2 when choosing a strategy, with proportions oscillating around 0.5 (Fig. 2.c). In scenario 3, populations consistently evolved to choose a kleptoparasitic-scrounger strategy in the presence of handlers (Fig. 2c.). This proportion was reduced at very low growth rates ($r_{base} < 0.01$; Fig. 2.c).

Spatial Distribution of Individuals and Prey

Individual Distributions. There number of individuals on a cell increased with its growth rate r, but there was substantial variation across cells with the same r. This variation was larger with increasing r since there were fewer cells with higher r. In the producer-only case, individual abundance showed a linear increase with cell quality, with the slope increasing with the simulation growth rate r_{base}. When two strategies were allowed however, there were strong differences in how they were distributed across cell qualities. In the fixed-strategy case, the abundance of producer individuals was uniformly low across cell qualities, while the abundance of scrounging kleptoparasites had a sigmoidal relationship with quality, mediated by r_{base}. In the flexible-strategy case, the use of either strategy was nearly invariant with cell quality. At very low r_{base} (0.001) the kleptoparasitic strategy was more ofen used than the producer strategy, while at higher r_{base}, the producer strategy was more common across cell quality.

Consequences for Prey Item Distribution. The distributon of items G varied considerably between scenarios and simulation-specific baseline growth rates r_{base}. In the **first scenario** G was insensitive to r, and items were uniformly distributed across cells of different growth rates. G was not signficantly different among simulations with different r_{base}. In the **second scenario** G increased strongly with r, and the curve of G r varied with r_{base}. The G r transformed from roughly linear (r_{base} = 0.001), to exponential (r_{base} = 0.01), and finally to sigmoidal ($r_{base} \in$ 0.03, 0.05) [see Figure

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276 X]. In the **third scenario** G varied only weakly across cells with different r, and the G r response

277 had a positive slope only for the highest r_{base} of 0.03 and 0.05.

Generalised Functional Response

279 The model coefficients of G and $N_p + N_s$ changed non-linearly in relation to r_{base} (Figure X). In

280 the producers-only case, the coefficient β_2 increased with r_{base} when $r_{base} \leq 0.03$, after which it

281 decreased below zero for r_{base} = 0.25. Similarly, the coefficient of items β_1 was highest at r_{base} =

282 0.03, decreasing to zero for r_{base} = 0.1 and 0.25. In the fixed-strategy case, β_1 (items) was at or near

283 zero across all r_{base}. However, β_2 for both W_p and W_s was near zero for $r_{base} \leq 0.05$, positive for

284 $r_{base} \in 0.075, 0.1$, and zero for r_{base} = 0.25. In the flexible-strategy case, both β_1 and β_2 showed a

285 hump-shaped relationship with r_{base} for both W_p and W_s, with the highest values at intermediate

286 growth rates.

Discussion

Conclusion

Acknowledgments

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Appendix A: Supplementary Figures

Fox–dog encounters through the ages

Appendix B: Additional Methods

Measuring the height of fox jumps without a meterstick

Tables

Figure legends
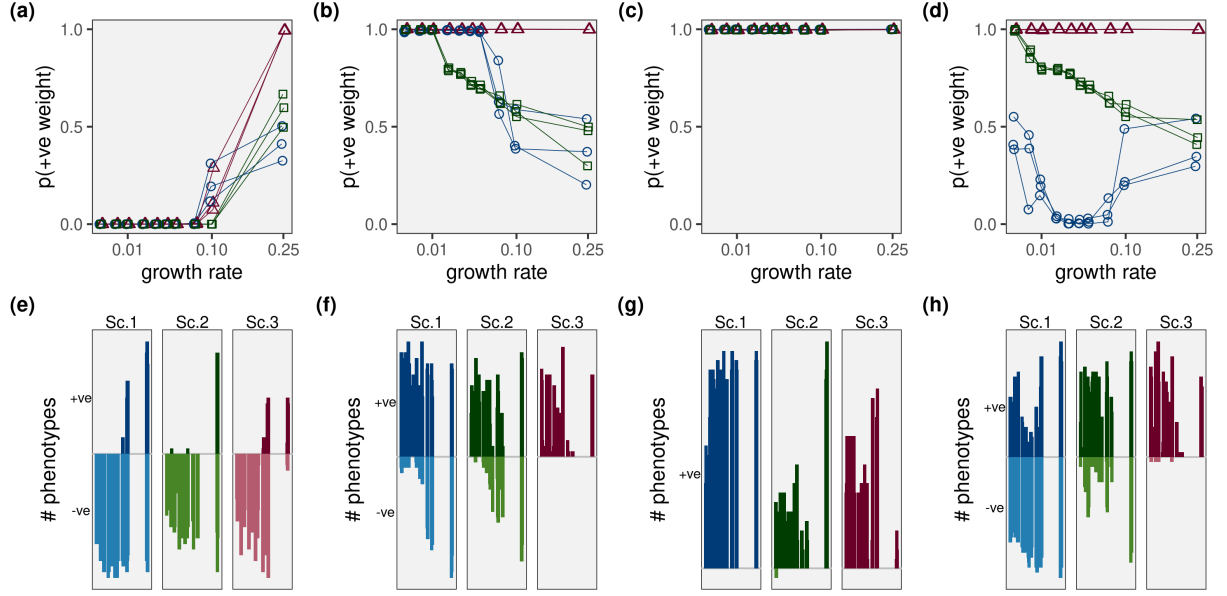
Online figure legends

Figure 1: Proportion of individuals in populations evolved across different regrowth rates selecting *for* environmental cues in deciding movement. Panels **(a – d)** show the proportion of individuals with positive weights for each cue: **(a)** non-handling individuals, **(b)** handling individuals, **(c)** prey items, and **(d)** individuals overall. Colours and shapes represent scenarios (blue circles: *producers-only*; green triangles: *fixed-strategy*; red squares: *flexible-strategy*). While lines connect similarly numbered replicates across r_{base}, these are entirely independent simulations. Panels **(e – h)** show the number of distinct values for each weight in the population in panels **(a – d)** separated by the sign (positive or negative): **(e)** non-handling individuals, **(f)** handling individuals, **(g)** prey items, and **(h)** individuals overall. Bar colours represent scenarios (blue: *producers-only*; green: *fixed-strategy*; red: *flexible-strategy*), while the hue represents the sign (light: positive, dark: negative). Individuals avoid non-handlers for $r_{base} \leq 0.1$, after which they evolve neutrally in scenarios 1 and 2, and strongly positive values in scenario 3 **(a, e)**. Similarly, most individuals in scenarios 1 and 2 move towards handlers, but the proportion and diversity of negative weights increases at $r_{base} \geq 0.1$ **(b, f)**. Individuals in scenario 3 consistently move towards handlers, and individuals overall **(b, f, d, h)**. Overall, in scenario 1 individual preference for moving towards other individuals has an inverse-humped relationship with r_{base}, while in scenario 2 it shows a steady linear decline.
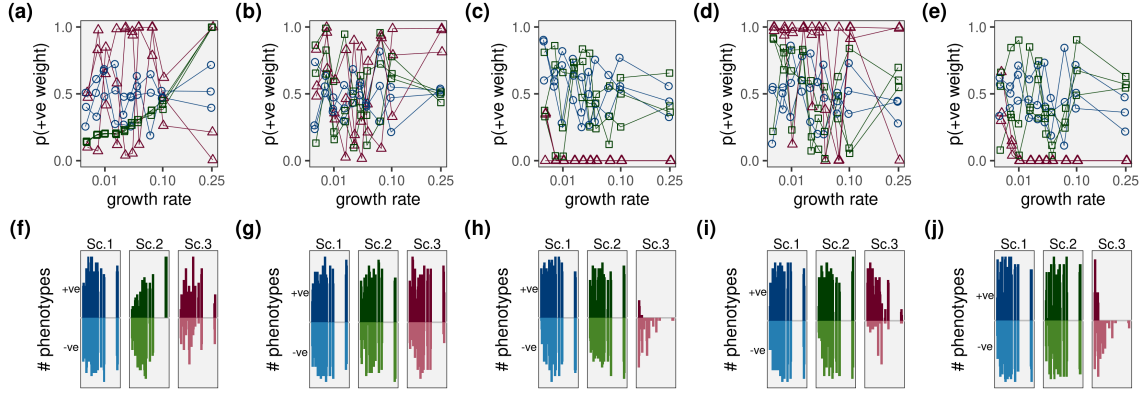
Figure 2: The proportion of individuals choosing a foraging strategy based on environmental cues is not linked to the regrowth rate. Panels **(a – e)** show the proportion of individuals with positive weights for each cue: **(a)** bias, **(b)** non-handling individuals, **(c)** handling individuals, **(d)** prey items, and **(e)** all cues combined. Colours and shapes represent scenarios (blue circles: *producers-only*; green triangles: *fixed-strategy*; red squares: *flexible-strategy*). Lines connect similarly numbered replicates across r_{base}, but these are entirely independent simulations. Panels **(f – j)** show the number of distinct values for each weight in the population in panels **(a – e)** separated by the sign (positive or negative): **(f)** bias, **(g)** non-handling individuals, **(h)** handling individuals, **(i)** prey items, and **(j)** all cues combined. Bar colours represent scenarios (blue: *producers-only*; green: *fixed-strategy*; red: *flexible-strategy*), while the hue represents the sign (light: positive, dark: negative). Individuals' weights in scenario 1 evolve neutrally since they are only allowed a producer strategy. However, scenario 2 also results in neutral evolution of all weights except f_b, with a larger proportion of individuals biased towards producing at high r_{base}. Almost all individuals in scenario 3 choose to steal except at very low r_{base}, with f_h the strongest contributor to the decision.