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Modelling migration in birds: competition's role in maintaining individual variation

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Animals exhibit extensive intraspecific variation in behaviour. Causes of such variation are less well understood. Here, we ask when competition leads to the maintenance of multiple behavioural strategies. We model variability using the timing of bird migration as an example. Birds often vary in when they return from non-breeding grounds to establish breeding territories. We assume that early-arriving birds (counting permanent residents as 'earliest') select the best territories. But arriving before the optimal (frequency-independent) breeding date incurs a fitness penalty. Using simulations, we find stable sets of return dates. When year-round residency is viable, the greatest between-individual variation occurs when a small proportion of permanent residents is favoured, and the rest of the population varies in their return times. However, when fitness losses due to year-round residency exceed the benefits of breeding in the worst territory, all individuals migrate, although their return dates often vary continuously. In that case, individual variation is inversely related to fitness risks and positively related to territory inequality. This result is applicable across many systems: when there is more to gain through competition, or when its risks are small, a diversity of individual strategies prevails. Additionally, stability can depend upon the distribution of resources.

1. Introduction

Individual variation in behaviour is widespread in natural populations [1–6], with many potential implications for evolutionary and ecological processes [7–11]. Nevertheless, mechanisms that underlie the origin and maintenance of behavioural variation are, in many contexts, not well understood [3]. Prior work has illustrated that frequency-dependent selection can promote intraspecific differences [12–15]. Here we build on this work by examining how frequency-dependent selection can create continuous variation in individuals' propensity to take risks.

Risk-taking during competition for resources is common, and often associated with variation among individuals [16]. Birds are excellent organisms to study individual variation in risk-taking because individuals of migratory species show extensive variation in timing their returns from non-breeding grounds to breeding grounds (we use these conventional terms, although other migration patterns exist) [17–22]. Birds that return earlier generally have higher reproductive success [18,23–27]. This may be due to earlier arrivals obtaining higher-quality territories, which can have a direct effect on reproductive output [25,28–31]. Thus, intraspecific competition may favour earlier arrival than might be optimal for abiotic conditions. Earlier arrival can increase mortality in bad weather [32] or incur energetic losses during suboptimal flight conditions [33]. Birds therefore face a dilemma between returning early to claim prime territory, and returning later to avoid risks. Unsurprisingly, birds have evolved many different strategies to deal with this trade-off. They can include complete migration by the entire population, partial migration by some members of the population, or completely non-migratory behaviour

[34,35]. The balance between risk and reward of arriving early will determine what proportion of the population migrates, and if they do migrate, at which times individuals choose to return.

Kokko [36] examined the distribution of early arrivals in a completely migratory population as a function of body condition. Other models have examined the effects of frequency and density dependence on partial migration [37–41]. In models of partial migration, only binary migrant/non-migrant strategies have been considered. Instead of limiting our analysis to either exploring the distribution of return times in a completely migratory population, or a binary migrant/non-migrant strategy set, in this study, we allowed multiple return strategies (times) to compete with one another to yield a pseudo-continuous distribution of return times. The resulting distribution describes both the proportion of individuals that migrate, and how the arrival of individual migrants varies. Thus, it provides us with insight into why many distributions in behaviour (normal, bimodal, etc.) are commonly exhibited by animal populations.

2. Methods

We envisage a population of birds that are identical except for their capacity to return at different times. We assume that a territory is required for successful breeding, and that territories are not equal in quality. We also assume that the bird that arrives first to a territory is always successful in defending it against later arrivals (i.e. a strong priority effect [42]), so it is never dislodged from a territory that it has settled on. We do not address sex-specific differences, although others have explored the evolution of protogyny and protandry (e.g. [43]).

For simplicity, we assume that the population size of breeding birds is fixed, and equal to the number of available territories. This can be interpreted as a population at its carrying capacity. We do not consider non-breeding individuals (e.g. 'floaters' without territories [44,45]). For each day that a bird arrives early from its non-breeding grounds relative to the optimal breeding date, it risks a loss of fitness [46]. Such losses include immediate mortality (starvation, predation, freezing, etc.), or another loss of fitness such as energy available for breeding or surviving the next migration. We consider a baseline fitness risk per unit time r, so the maximum possible fitness a bird arriving x time units early can achieve (independent of competition) is described by $f(r, x)$. We use the function $f(r, x) = (1 - r)^x$, where r is constant (figure 1a). By choosing a constant risk per unit time, we implicitly assume a step function in which risk to birds on the breeding grounds is r (per unit time) during the non-breeding season, and 0 during the breeding season (relative to residing on the non-breeding grounds). Initial exploration of accelerating risk functions yielded similar results, and we did not pursue them further. Time ranges between 0, the optimal arrival time in the absence of competition, and x_{max}, the earliest possible arrival. One can think of this as a countdown from x_{max} to 0, when breeding begins. When r is so high that arrival at x_{max} is inviable, x_{max} can be interpreted as a boundary imposed by environmental conditions on the earliest possible return date (hence, the entire population must be migratory). When r is low enough that birds can arrive at x_{max}, it is reasonable to interpret arrival at x_{max} as remaining on the breeding grounds all year. In such a case, x could represent months. Alternatively, one could interpret a scenario where individuals arrive on x_{max} as representing a case where the population is completely migratory, but there is a hard barrier to earlier arrival, such as prevailing (and unfavourable) seasonal wind conditions that prevent flight or make earlier migration too dangerous. Irrespective of which of these interpretations is
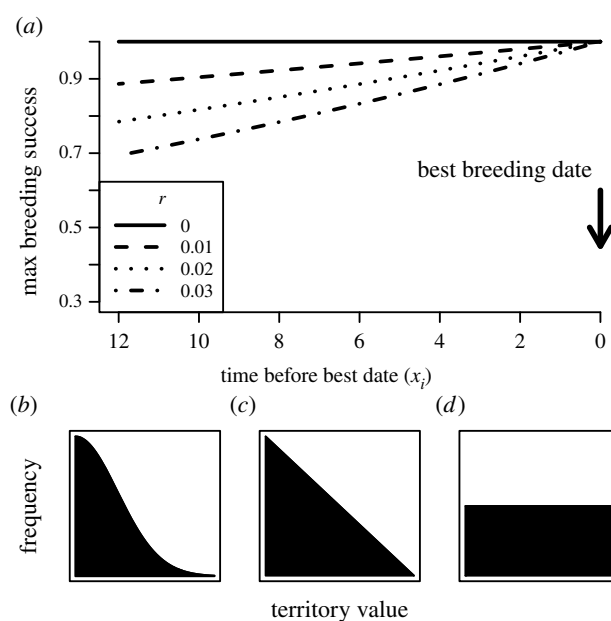
Figure 1. (a) Expected maximum breeding success across x time units of early arrival, assuming that no other birds arrive at that time. The risk per time unit, r, controls how quickly losses accumulate with x. Each time unit x upon which a bird can return is also a strategy in our model. (b–d) Distributions from which we drew territories to examine the sensitivity of our model. (b) Right half of the normal distribution. (c) Number of territories decreases linearly with quality. (d) Uniform distribution.

chosen, birds using the x_{max} strategy claim the best territories. We chose a modelling framework with this flexibility of interpretation so that it might apply, at least heuristically, across many different systems. For example, migration can feature populations travelling huge distances *en masse* between breeding and non-breeding grounds [21], but also loosely timed, continuous shifts in range [47], or comparatively small translocations in elevation [48]. Empirical results on the genetics of migration show high levels of heritability and adaptive potential in migration, so our continuous approach is appropriate. Three to six generations of artificial selection on partially migratory lines of blackcaps (*Sylvia atricapilla*) produced completely migratory or non-migratory populations, while only two generations of selection were necessary to shift migratory timing by a period of two weeks [49,50].

At each time in the migration window, starting with x_{max}, n_x birds arrive on the breeding grounds to claim the best n_x territories. This continues for each time unit till there are no territories left (which happens on the optimal breeding commencement date, at the latest). All birds that arrive at the same time obtain the same fitness: the mean quality of the best n_x territories available multiplied by the maximum fitness $f(r, x)$ that they could achieve by arriving at that time (the same result would be obtained by explicitly assigning them at random to the best n_x territories). Each bird's fitness depends therefore not only on how early it arrives, but also on how many other birds arrive with it. If any individuals in the population are using the x_{max} strategy (and hence are non-migrants under one interpretation), they claim the best territories.

Determining optimal arrival dates requires measuring the success of each strategy against all others across many different frequencies of each arrival date in the population. We sought a vector of arrival dates that described the frequencies of strategies within a population, which would be robust against invasion by other strategies. The *number* of strategies (not *values*) that could coexist at equilibrium had a possible range of 1 to $x_{max} + 1$.

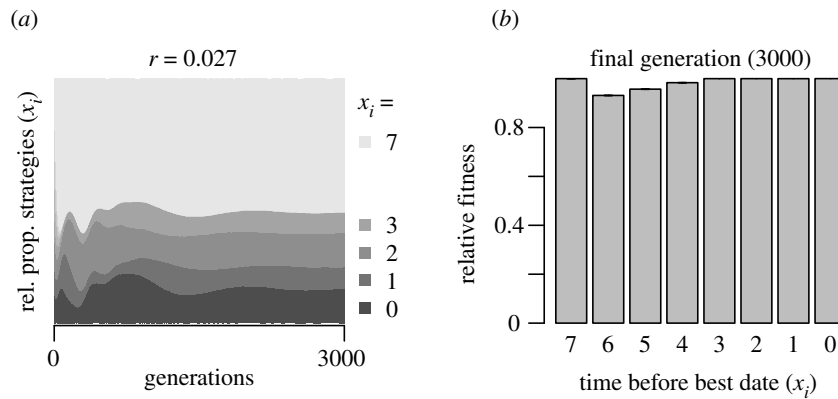We used simulation modelling to examine a wide range of strategy space under different assumptions, and confirmed the

Figure 2. (*a*) Across 3000 generations, the relative proportion of each possible strategy is shown by the width of the shaded segments. Arrival on x_{max} is the lightest colour, and dominates approximately half the population by generation 3000. (*b*) In the final generation, relative fitness was approximately 1 for strategies above a threshold frequency. Error bars are 95% confidence intervals bootstrapped from five runs.

results of our simulations with analytical methods for some of the simplest sets of assumptions. The simulation method that we used was designed to approximate solutions to the replicator equation that, in game theory, describes how strategies compete with one another [51]. We began with populations in which strategies had randomly chosen frequencies. We generated a sample population from these initial frequencies of arrival dates. If a strategy did not appear in the sample population, we created additional populations until it did (this rarely occurred, as the population contained 30 000 individuals). We calculated the relative fitness of strategies and then updated each strategy's frequency by multiplying its old frequency by its relative fitness. Strategies were prevented from going completely extinct by setting a (very small) minimum probability with which they could appear. This allowed us to approximate the 'invasion fitness' (fitness when rare) of each strategy against the set of existing strategies. We repeated this process across 3000 generations. When 3000 generations were insufficient to produce convergence, we extended the run time to 10 000 generations, which was sufficient for convergence, except when territories were drawn from a uniform distribution.

In our simulations, we explored strategy sets over a range of values for r, the difference between the best territory and the worst territory (t_{min}) (without loss of generality, we fixed the best territory as having a payoff of 1), the number of strategies possible (x_{max}), and the shape of the distribution of territories. We considered territories drawn from a uniform distribution, from a distribution where the number of territories increased linearly with decreasing quality (hereafter, 'linear'), and from the right half of a normal distribution, where 70% of territories are in the bottom third of the range (figure 1*b*–*d*). The uniform distribution is the simplest and best-explored by other studies (e.g. [38,39]). It was also suitable for analytical modelling. However, it is highly unrealistic, since habitats of different quality are unlikely to be equally represented in the environment. Instead, it is more likely that some areas will be optimally suited to a species's niche, whereas much of the available land will be poor [30]. We used the linear distribution and the right half of the normal distribution to increase the biological realism of the simulated territories.

In our analytical model, we assumed that territories were drawn from a uniform distribution with maximum b and minimum m, so that they decreased in quality from b to m according to the line $b - m \times arrival\ order$. We assumed only three strategies were possible (early, middle and late), and that their respective frequencies summed to unity ($x_1 + x_2 + x_3 = 1$). Risks to arriving before the optimal breeding time were governed by the same function $f(r, x)$ as in the simulation model. We found the equilibria of the replicator equation that follows from these assumptions, and analysed their stability using standard methods [52,53].

3. Results

We present output where $x_{max} = 8$ and territories were drawn from the right half of the normal distribution. When $x_{max} = 8$, the time units could reasonably be interpreted to represent the number of months in the year outside of the breeding season. Strategies that remained above the minimum threshold to be considered present in the population (arbitrarily set at a fraction 0.005 of the most abundant strategy, to exclude strategies present due to drift) had relative fitness near 1 (e.g. figure 2). This is consistent with frequency-dependent selection favouring the coexistence of different strategies.

Arriving on x_{max} is only a viable strategy when $f(r, x_{max}) > t_{min}$. Under such conditions, one useful interpretation is that individuals arriving on x_{max} have remained on the breeding grounds as non-migratory residents. With this interpretation, figure 2 would represent a partially migratory population. Typically, there was a gap between non-migrants and the earliest return by actual migrants. Intuitively, it would make little sense for a bird to invest in migration only to immediately turn around and begin flying back to compete for its territory. Our model captures this realistic pattern, although it does not include an explicit cost to the act of migration itself—the bimodality in the distribution is driven entirely by frequency-dependent selection for investment in risks to fitness. When we added a cost for migration to our model in the form of a constant fitness penalty that individuals had to pay for using a strategy other than x_{max}, it had a disproportionately negative effect on intermediate strategies, causing a tendency towards even greater bimodality in partially migratory populations (electronic supplementary material, figure S1). Migrants (individuals not using the x_{max} strategy) tended to exhibit variability in their return dates (i.e. the multiple dark regions in figure 2*a*), which can only be driven by competition for breeding sites. This individual variability among migrants typically persisted when there was a penalty to migration, although it could decrease the number of migrant morphs at equilibrium (e.g. electronic supplementary material, figure S1).

Depending on the values of r and t_{min}, the set of strategies present at equilibrium could include only non-migratory residents (figure 3, yellow), all birds migrating and arriving on the latest possible date (figure 3, blue), or a polymorphic combination of arrival at various times, including both partial migration and variable arrival dates in completely migratory populations (figure 3, greens). In other words, a unimodal
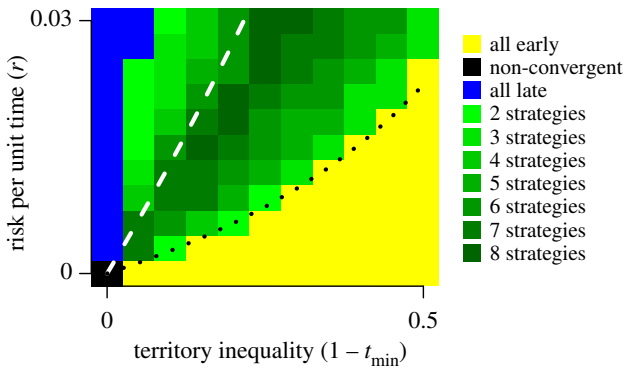
Figure 3. The number of strategies present in the population at equilibrium as a function of risk per unit time (r) and resource inequality ($1 - t_{min}$). The white dashed line describes $f(r, x) = t_{min}$, where fitness due to returning on the earliest possible date (i.e. being a non-migrant) is exactly balanced by the fitness expected for breeding on the worst territory if an individual returns from migration on the latest date. The black dotted line describes $f(r, x_{max}) \cdot t_{mean} = t_{min}$, below which the earliest arrival strategy is uninvadable. When there is no risk to arriving early, but all territories are equal, strategies drift randomly (black square). (Online version in colour.)

polymorphism could persist even when residency was not a viable strategy. It seems likely that bimodality is a consequence of the boundary imposed by x_{max}. The maximum number of strategies that could coexist was found when non-migration was a viable strategy ($f(r, x_{max}) < t_{min}$, below the white dashed line in figure 3), but the entire population did not evolve to become non-migrants because the cost of remaining on the breeding grounds was high enough to act as a deterrent. It was also necessary for territory inequality to be low, so there was not too strong a competitive incentive to remain a non-migratory resident. A reviewer has pointed out that additionally, when $f(r, x_{max}) \cdot t_{mean} > t_{min}$, where t_{mean} is the mean value of all territories, the strategy of arriving on x_{max} is uninvadable. This threshold is demarked with the black dotted line in figure 3. Below this line, all individuals should be non-migratory residents. Above this line, but below the white dashed line, is a region where partial migration can be maintained in the population. In the region above the white dashed line, the population is completely migratory.

In completely migratory populations, there were simple relationships between individual variability (i.e. polymorphism), risk and resource inequality: variability decreased with risk, and it increased with resource inequality. When there was more reason to compete, and less cost to doing so, it favoured a diversity of strategies for investment in competition. It would be difficult to predict from a simple model with two levels of competition whether intermediate levels of investment can persist, or whether only hypercompetitive strategies and non-competitive strategies can succeed. The natural cutoff imposed by the white dashed line at $f(r, x_{max}) = t_{min}$ can be interpreted as representing other, non-migratory competitive contexts where investment in risks are limited only by their costs. Results from this scenario suggest that intermediate phenotypes may often be maintained by selection.

Our results were robust to variation in x_{max} (electronic supplementary material, figure S2), with a trend for polymorphism to be maintained over a wider range of territory inequality as x_{max} increased. This is because risk was compounded over more time units, preventing early arrivers from excluding other strategies in the population. Naturally, if a population is subdivided into smaller time scales, one

would have to adjust r to compensate if one were doing empirical research. Results were also robust to the use of a linear territory distribution, but not a uniform distribution (electronic supplementary material, figure S2). Indeed, under the uniform distribution we observed only three outcomes: (i) all early arrival, (ii) all late arrival and (iii) non-convergence where dynamic fluctuations in strategies maintained variation across time (see electronic supplementary material, figure S3 for an example). Our analytical model revealed that all early arrivals, or all late arrivals were the only stable equilibria of the three-strategy system (full treatment is available in the electronic supplementary material in a Mathematica notebook and Julia file). Numerically solving the analytical equations yielded essentially identical results to our simulation model under the same parameter choices and starting points (electronic supplementary material, figure S4). This gives us confidence that our simulation results reveal meaningful behaviour of the system. In general, even though the simulation's qualitative behaviour was sensitive to territory distribution, individual variation was maintained for similar values of r and t_{min}. With normal and linear distributions, variation was maintained by stable sets of strategies; with the uniform distribution, variation was maintained through dynamic temporal fluctuations.

4. Discussion

Our results help explain widespread between-individual variation in risk-taking. Our model predicts that between-individual variation can adopt many distributions, including monomorphism, unimodality with high variability and bimodality. These patterns all occur in natural populations [35,54,55], suggesting that frequency-dependence could have an important explanatory role for maintaining individual differences in behaviour. If there is an upper limit to the amount that an individual can invest in competitive behaviours—for example, when it cannot arrive to breed any earlier, and instead remains a year-round resident—resource inequality or low costs of competition can create a monomorphism where all individuals are maximally competitive (e.g. non-migratory, below the black dotted line in figure 3) [38,39,41]. Maximal between-individual variation is found when the costs of investment in competition are slightly less than the benefits of the worst resource (just below the dashed line in figure 3, where populations contain non-migrants and a mixture of migration return times). If investment in competition is only limited by fitness costs (rather than a hard constraint like earliest arrival date, above the dashed line in figure 3a), a diversity of strategies is maintained whose richness diminishes with resource equality and increasing risk, which both disfavour competition. Predictions from this latter case may be easily testable in experimental settings, which do not have to involve migration, but could instead use other behaviours or traits associated with intraspecific competition for the same resource type. Many sexually selected traits probably fit this description (e.g. the horns of rhinoceros beetles [56]).

The modelling approach we used is agnostic about the mechanisms by which behavioural variability is produced. In the real world these distributions of behaviours could be produced by canalized or plastic mechanisms. Among migratory animals, both repeatable individual variation (due to fixed differences, or plastic differences that are only

labile early in development) and unpredictable individual variation in migratory timing have been documented [20,21,57–59]. One scenario that might favour genetic control of a trait is when individuals must decide to leave their non-breeding grounds, but have no way of accurately assessing conditions on breeding grounds thousands of miles away. Additionally, when individuals cannot observe one another make decisions to leave non-breeding grounds, it may be difficult for individuals to accurately assess how many competitors they will face. Such difficulty in assessment might favour genetic control and consistent individual differences in migration. However, if large-scale weather patterns make climate on non-breeding grounds a predictor of climate on the breeding grounds (e.g. the El Niño Southern Oscillation [60]), there is scope for plastic adjustment of migration. Furthermore, when individuals have the capacity to assess the potential competition on the breeding grounds—for example, by observing the number of migrants departing from non-breeding grounds—plastic control may also be favoured.

Outside the phenomenon of migration, consistent individual differences in behaviour (i.e. animal personality) are highly heritable [61–63]. The evolution of personalities can be favoured when individuals repeatedly expressing the same behaviour decreases its cost [14]. However, genetic control of a trait could also be favoured if the environment is difficult to accurately assess, or if there are other costs to phenotypic plasticity [64], and accurate assessment is critical for making an appropriate investment in risky competitive behaviour [65,66]. Future investigation on this topic would at minimum need to include a parameter that controls an individual's degree of adjustment to local environmental conditions as well as a function that maps environmental conditions onto phenotype.

This study is one of a few to examine under which conditions an indeterminate number of strategies can coexist. Baldauf et al. [15] built a model in which individuals could invest a continuous amount into competition. In other words, strategy space in their model was continuous rather than discretized as in our model. The resources that individuals competed for were either high or low in quality. Baldauf et al. [15] found monomorphism, bimodality, or cyclic behaviour that depended on the relationship between stochastic error in resource acquisition, mean resource quality, and resource inequality. These outcomes are similar to what we observe with a uniform territory distribution, although we did not find stable bimodality there. In general, however, our results are conceptually similar to those of Baldauf et al. [15]: strong resource inequality favours maximal investment into competition, eroding variation. In nature, we suspect that the resource distributions we used may be more realistic representations of the ecological niche that animals must occupy. The niche is often conceptualized as a narrow optimum in multidimensional space, and individual fitness is assumed to drop off with displacement from the optimum [67,68]. Thus, lousy resources are likely to be much more abundant that excellent ones. The stable polymorphisms that our model generates under the normal and linear distributions may characterize evolutionary responses to costly competition for relatively stationary ecological resources, for example breeding territories. Our results under the uniform distribution and those of Baldauf et al. [15] may better represent situations when resource value diminishes in linear order from more competitive to less competitive individuals. Systems of sexual selection where mating is decided by competition may be better described by such distributions—if mating opportunities are linear functions of an individual's rank in the population.

In modelling migration, our study is preceded by Kokko [36], who elegantly applied game theory to model the arrival dates that resulted from competition among migratory birds. In that model, a continuous distribution of arrival dates could arise, including unimodal and bimodal forms, although partial migration was not included in that study. The mechanism by which competitive ability arose was also different: some birds were in superior condition to others, and thus could invest more in early migration than others. The solution to the game theoretical dilemma faced by each bird rested on arriving just early enough to deter the next-worst bird from stealing the best remaining territory. This is clearly very different from our assumption of uniformity among individuals except for arrival date, and for some systems, Kokko's [36] assumption certainly captures an essential element of realism. Our examination of frequency-dependent selection acting alone is thus complimentary to Kokko [36]. Frequency-dependence is sufficient to produce a similar pattern, which suggests that between-individual variation in arrival dates can arise even when differences in competitive ability are not created by environmentally mediated differences in condition. Kokko [36] additionally explored conditions we did not, such as imperfect assessment of territory quality, and usurpation of territories after an owner has died. These additions tend to lessen the strength of competition to arrive early. Harts et al. [69] investigated the effect of predation risk upon migrants, which favoured uniform arrival dates.

Several models have looked at partial migration (with non-migratory residency and complete migration as extremes) [38–41]. These models consider binary migratory versus non-migratory strategies. They also examine density- as well as frequency-dependent selection. Our model was designed with different aims in mind, although partial migration is an interpretation of our model when some individuals arrive on x_{max}, and partial migration therefore emerges as part of the distribution of individual behaviours. In all models where partial migration is possible, including this one, competition is a critical determinant of the decision to migrate or not.

In sum, we have shown how frequency-dependent selection can create continuous distributions of individual variation in risk-taking behaviours. This happens even when individuals are competing with one another for a single resource of variable quantity (i.e. habitat productivity), rather than adapting to exploit different kinds of resources along a continuous distribution (e.g. [70,71]). Thus, the scramble for a narrow band of resources may create many different behaviours all selected to play against one another.

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