

To play or not to play? That's a resource abundance question

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Abstract

18 Although play occurs in a wide variety of animals, models of the origins of play behavior are
19 lacking. We propose a novel computational model exploring the evolution of non-social
20 frivolous play. Asexually reproducing semelparous animals can either rest or forage. Foraging
21 occurs when an organism is below an energy threshold. Success is determined by the
22 combination of skill and availability of resources, which declines over time but replenishes for
23 each generation. Play was introduced as a mutant strategy: a frivolous activity that uses energy
24 and increases the probability of dying over resting with no direct fitness benefit. Simulations
25 show that play behavior becomes fixed in the population and the time spent playing is
26 maintained at a low rate in spite of its costly nature. When play behavior is functional by
27 increasing foraging ability, it evolves quickly and the time individuals spend playing increases,
28 but eventually the population of players collapses and play disappears. We suggest a mechanism
29 underlying the origins of adaptive play from non-adaptive behavior when resources expand.
30 Initially play acts as a spiteful behavior in that playing individuals suffer a direct cost to their
31 fitness, but also may incur even greater costs to other individuals in the population.

32

Introduction

There have been only a few attempts to model play behavior in the literature (citations in Burghardt, 2005; Pellis, Burghardt, Palagi, & Mangel, this issue) and no models we are aware of deal with the origins of play and how it could become established in the first place. Progress was hindered by an unclear conception of what play was, how to identify it, and confusion among different types and complexities of play (Burghardt, 2005). We now have a set of 5 criteria for identifying play in diverse species and contexts, allowing play to be identified in animals ranging from invertebrates (e.g. octopus, spiders, insects) to members of all vertebrate classes (Graham & Burghardt, 2010; Burghardt, 2014). A recent brief statement (Burghardt, 2014: 91) is: *Play is repeated, seemingly non-functional behavior differing from more adaptive versions structurally, contextually, or developmentally, and initiated when the animal is in a relaxed, unstimulating, or low stress setting*. Thus, while play is certainly most common and complex in many mammals (e.g., primates, rodents, carnivores, cetaceans) and birds (e.g., corvids, parrots, raptors) the fact that it occurs in diverse and distantly related taxa raises the issue of the origins of such behavior multiple times over the course of animal evolution.

Another advance was to recognize that play may be classified into three processes, primary, secondary, and tertiary (Burghardt, 2005). Only the first is relevant to the origins issue, as such play is a byproduct of various factors such as high metabolic energy, boredom, motivational conflicts, incipient (intention) movements, and other ethological and psychological factors (see Pellis et al., this issue). Here we use a very simple system to model the behavior of animals engaged in seemingly nonfunctional, but somewhat costly, behavior or not doing so, and exploring if and how play becomes established in the population. Play in animals is typically divided into locomotor, object, and social play, and can be quite complex, especially the latter.

Here we focus on nonsocial play in a simple system, with the hope that more realistic models and research testing hypotheses in more naturalistic contexts will be fostered. We are attempting to construct models in which play can not only originate, but become established and be maintained in a population, even if the time spent playing is at a low rate.

We are using as our conceptual source Surplus Resource Theory (SRT) as developed in several places over the last decades (e.g., Burghardt, 1988, 2005, 2014; Pellis et al. this issue). SRT postulates that abundance and variety of resources (e.g., energetic, behavioral) are important for play behavior; empirical work has shown that play can be very costly in terms of energy use (e.g., Martin, 1984; Miller & Byers, 1991; Burghardt, 2005). Although much modeling attention has been given to resource abundance and foraging, growth, reproductive rates, and territorial behavior (Fretwell, 1972; Smith, 1982; Dugatkin, 2013; Dugatkin & Reeve, 2013), little modeling has been done for play behavior (Dugatkin & Bekoff, 2003; Grunloh & Mangel, this issue).

A general finding motivating our approach is widespread evidence that limited food resources reduce or even eliminate play in many animals (reviewed in Burghardt, 2005); in fact, play is usually the first behavior dropped from a species' repertoire when survival conditions are unfavorable. In the following model, then, the 'animal' population is in an environment with food resources of a fixed amount, that are only replenished 'seasonally' as often occurs in natural settings.

General overview of the model

Individual-based models (IBMs) allow for inclusion of a vast array of detail concerning individual behavior and characteristics in determining population

response (Judson, 94; Grimm, 2005; DeAnglelis & Mooij, 2005). They have been particularly important in situations in which interactions between individuals affect population response, notably when these interactions are affected by spatial aspects of the environment or the interactions depend upon the characteristics of the individuals involved, such as their size, social status, or genetically influenced behavioral traits such as shyness, boldness, and aggressiveness (Grimm, 2005). IBMs are formulated based upon sets of rules for changes in state of individuals, with the rule set chosen to represent general responses (e.g., to address fundamental questions such as the nature of spatial patterns that arise from different individual movement rules) or responses of particular species of interest. In the latter case, rules are chosen from observation and the model may be evaluated through comparison with field or laboratory data. Dependence of rule sets upon such data provides one of the challenges to developing IBMs in that available data may be too sparse to account for the range of possible individual responses. In this case, we develop our IBM from a theoretical perspective to begin teasing apart primary drivers of the evolution of play behavior.

Our initial model is a non-spatial agent-based model where individuals indirectly compete for a fixed amount of resources in their environment over a given time period. Individuals can rest, forage or play (given that they have the genetic disposition to do so). Note that ‘play’ is initially equated with non-functional but energy consuming behavior. The other behaviors of resting and foraging are both energy consuming (and have associated mortalities), but foraging leads to energy acquisition and not just expenditure. Play behavior is introduced as a mutant and can come in two flavors, frivolous (without any direct benefit) or non-frivolous

(having a foraging benefit). This is realistic to the extent that object or locomotor play may improve hunting or foraging behavior, directly or indirectly (Burghardt, 2005).

Methods

The intent of the model was to explore under what conditions play behavior emerges in a population of non-social organisms that spend their time resting, foraging or playing (if they have the genetic propensity to do so). The model begins with a fixed population size of Non-Player Agents (NPAs) whose behavior is limited to foraging a limited resource or resting at each time step (t), and the initial amount of available resources ($\rho(0)$) in the environment is finite for a given reproductive time period (T). NPAs start their life cycle with an initial energy level ($E_i(0)$), will attempt to forage when their energy reserves fall below a given hunger threshold ($E_i(t) < \alpha$) or will rest otherwise. Resting uses c units of energy and has an associated probability of dying (ψ):

$$\begin{aligned} E_i(t) &= E_i(t-1) - c, \\ \rho(t) &= \rho(t-1). \end{aligned} \tag{1}$$

The probability that a foraging attempt is successful at time t is determined by:

$$f(t) = \beta \left(\frac{\rho(t)}{\rho(0)} \right), \tag{2}$$

where (β) is the foraging ability and $\rho(t)/\rho(0)$ the availability of resources in the environment at the given time step. Foraging ability ($0 < \beta < 1$) can be viewed as the probability that an organisms catches a prey or finds a food source, and as β approaches 1 the organisms is a better forager. This model does not have an explicit spatial component, meaning individuals do not have a location relative to other organisms or with resources. So foraging only depends on the

current amount of resources in the environment and the individuals foraging ability. A successful foraging attempt results in κ energy gain and a reduction of a resource in the environment,

$$\begin{aligned} E_i(t) &= E_i(t-1) + \kappa, \\ \rho(t) &= \rho(t-1) - 1, \end{aligned} \tag{3}$$

while unsuccessful foraging result in energy cost φ , with $\varphi > c$:

$$\begin{aligned} E_i(t) &= E_i(t-1) - \varphi, \\ \rho(t) &= \rho(t-1). \end{aligned} \tag{4}$$

Foraging and resting also have an associated probability of dying, η and ψ respectively, with $\eta > \psi$, and having no energy ($E_i(t) \leq 0$) leads to an immediate death (see Figure 1). After a given number of time steps the surviving NPAs asexually reproduce, with fitness as a function of their energy level at the end of their life cycle, and die. Resources are replenished at the start of the next generation.

Figures 1 and 2 here

Play behavior is introduced as a heritable behavior and is modeled with two loci. The first locus is binary in character and determines whether or not play occurs, while the other is a quantitative trait that determines how often the individual plays. The life history of the player agents (PAs) is similar to the NPAs (see Figure 2), except that when the PAs are satiated they play with probability π_i ($0 \leq \pi_i \leq 1$). This play behavior has an energy cost, λ , such that $\varphi > \lambda > c$, and probability of dying, θ , such that $\eta > \theta > \psi$. The probability of foraging success is now a function of play frequency:

$$f(t) = [\beta + (1 - \beta)\gamma\pi] \left(\frac{\rho(t)}{\rho(0)} \right), \tag{5}$$

where γ is the parameter that controls how much play behavior effects foraging ability ($0 \leq \gamma$ and when $\gamma = 0$ there is no foraging benefit from play). Formulating the model this way ensures

that the probability of foraging success is between 0 and 1 when $0 \leq \gamma \leq 1$, but results in diminishing returns for playing when foragers ability increases. This effect is negligible except for the unrealistic case when organisms are poor foragers ($\beta \ll 1$) and play all of the time they could spend resting ($\pi \approx 1$). Successful foraging for PA results in an increase of κ energy and a removal of a resource from the environment.

Table 1 here

Differences in individual fitness are determined by individual energy levels at the end of the reproductive period ($t = T$) and individual fitness (w_i) is calculated:

$$w_i = w_0(1 - s) + s \cdot E_i(T), \quad (6)$$

where w_0 is the baseline fitness for the population and s is the selection coefficient. Weak selection is imposed (Burger, 2000) and the expected number of offspring for each parent is calculated using their relative fitness, $w_i/\bar{w}$ (where $\bar{w}$ is the average fitness for the generation), to ensure the initial population size is constant for each generation. Play is introduced as a mutation with all organisms initially not playing ($\pi_i = 0$). The play gene is turned on or off through mutation and the amount of time an individual plays is increased (or decreased) by a mutation effect (μ_e):

$$\pi_i = \pi_p \pm \mu_e, \quad (7)$$

where π_p is the parental play time and if $\pi_i < 0$ then $\pi_i = 0$. Formulating play genetics this way ensures that even if individuals spend a large amount of time playing (i.e. $\pi_i \gg 0$), they can still lose the ability to play by random mutation.

To determine the hunger threshold, simulations were conducted for a given set of parameter values seeded with different hunger thresholds. The maximum of these values that maintained the population size (i.e., the population survived T time steps) was used for the main

simulations. All simulations were run with MATLAB and the parameter values explored are found in Table 1.

Results

The main result of the model simulations is that frivolous play evolves in a population when there are ample resources, and that even when there are ample resources, non-frivolous play can only be maintained (i.e. fixation occurs) in the population for a small set of extreme parameter values (e.g., a large energy cost to play). Other results from these computational simulations show that play can emerge and be maintained in a population even when play does not have a direct fitness benefit and play has a greater energy cost than resting (see Figure 3A). When play does have a benefit, (i.e., the more the organism spends time playing, the better they are at foraging), play also evolves, yet cannot be maintained in the population, even when play gives a small benefit to foraging (see Figure 3B). Play behavior becomes more frequent and more variable before it reaches some threshold in the population, then it disappears and the cycle starts anew (see Figure 3B).

Figure 3 here

Different parameter values were explored for the costs of playing (λ), the initial amount of resources in the environment ($\rho(0)$), foraging ability (β), and play foraging benefit (γ), resulting in different average play time for the population and frequency of the play gene in the population. Increasing the cost of play and reducing the amount of resources greatly increases the time that individuals play yet reduces the average number of individuals that play in the population (see Figure 4). When play is maintained in the population, the average amount individuals spend time playing instead of resting is very small ($\pi \leq 0.05$). Initial resource

abundance appears to be the most important parameter for the emergence and maintenance of play in the population (see Figure 4). As play behavior becomes more frequent and play time increases it has a significant impact on the amount of available resources in the environment over the course of the individual's life cycle (see Figure 5). Even a small amount of play time reduces the amount of resources available for the entire population, and therefore reduces the number of successful foraging attempts for everyone. This is even more costly for those who do not spend any time playing, since they do not become hungry as frequent as the players (since the cost of resting is much less than playing) and fail to take advantage of resources when available. Increasing costs to rest and decreasing the amount of resources results in less time the organisms play, while decreases in resources and increases in the cost to rest reduces the play gene frequency despite it still becoming fixed in the population once it invades (see Figure 4B).

Figure 4 here

There is a strong relationship between play behavior and resource dynamics (Figure 5): organisms that play use more energy and therefore get hungrier more quickly than non-players and reduce the available resources more quickly than a population of non-players. There is a non-linear effect on this depletion of resources, with the amount of time spent playing having a stronger effect than the proportion of the population who play. When $\pi > 0.5$ resources deplete within a few time steps after the season begins (see Figure 5B).

Figure 5 here

Discussion

The results show play evolving and becoming fixed in the population where there is no direct fitness benefit to engaging in play, and even though play incurs direct costs of

206 increased mortality and energy use. This finding implies that there must be an indirect
207 benefit of play for it to both arise and be maintained in a population. The bar plots of
208 Figure 4 show that resource abundance in the environment is the most important
209 parameter of the model to explain the emergence of play behavior, followed by the
210 energetic costs of playing. Ironically, it appears that non-functional play acts as a spiteful
211 behavior in that playing individuals suffer a direct cost to their fitness, through an
212 increased probability of dying and energy use, but may also incur even greater costs to
213 other individuals in the population (Hamilton, 1964, 1970).

214 In this model the relation of play behavior to the amount of resources in the
215 environment is clear (see Figure 5). The mechanism at work seems to be that those
216 individuals who play get hungrier (i.e. need resources) sooner than those who rest,
217 resulting in their foraging more often and more quickly. This reduces the amount of
218 resources available in the environment, leaving the non-players less likely to effectively
219 forage and resulting in their having fewer offspring. There is also an upper limit to how
220 much individuals should play, since they can deplete the environment too quickly and
221 die. This is similar to pathogen virulence; if a pathogen becomes overly virulent it can
222 kill the host (Goodnight et al., 2008). This scenario occurs when there is a direct fitness
223 benefit to play, namely that the more an individual plays the better at foraging they
224 become. Play evolves more quickly in the population, but then disappears after an arms
225 race to play more and more often results in a depletion of resources which cannot sustain
226 the population. Thus, it is not only the amount of resources in the environment, but how
227 quickly the population depletes them. If we were to allow for unlimited resources or
228 resources that did not decline as they were consumed, then we would not expect the

229 above scenario to occur, but for play not to evolve since it is costly in terms of energy
230 usage and an increased probability of dying.

231 The results might explain why play rarely seems to have a runaway effect. In fact,
232 many human moral lessons point out that if everyone in a society engaged in
233 nonproductive activities (sports, arts, theatre, religion, video games, etc.) in terms of
234 resource acquisition, the society could not be maintained, as no members were producing
235 the resources necessary for such otherwise socially and personally enriching activities.
236 Play is, however, both a measure of freedom and a source of creative achievement
237 (Burghardt, 2013; 2015). The irony is that our initially non-intuitive results from the
238 novel model suggest that play could have originated as a selfish, even spiteful behavior,
239 *en route* to becoming a socially and reproductively valuable activity.

240 This model provides a possible key to the puzzle for the evolution of apparently non-
241 functional nonadaptive behavior. Is this also supported biologically? If the playing animals are
242 operating as if they have a higher metabolic rate, they are overall more active and thus exploiting
243 environmental resources at a higher rate than less active animals, and a relationship between
244 metabolic rate and play has been often proposed and supported (Burghardt, 1984, 1988, 2005).
245 Thus, under certain conditions, animals with higher metabolic rates or more complex and
246 energetically costly behavior and physiology, may be more evolutionarily successful than species
247 with fewer requirements for survival. This may relate to the observation that terrestrial
248 endothermic vertebrates generally out-compete ectothermic vertebrates, such as reptiles,
249 competing for similar resources. But, in deserts, for example, where food is often limited both in
250 amount and seasonally, reptiles are often more successful, numerous, and speciose.

Future directions for the model include, but are not limited to, variability in initial resource availability within and across generations (to simulate seasonal, environmental variability), overlapping generations, reproduction not dependent on time but after reaching an energy threshold, a spatial component, social play, direct competition for resources (e.g. hawk-dove interactions), and predator-prey interactions. A construction of the model accounting for kin-selection and non-random mating is another possible avenue for future research. The formulations of this theoretical model offer experimenters and empiricists the opportunity to test numerous hypotheses about the relationship between resource abundance and play behavior. The parameters of this model are intuitive and observable for different species, allowing this model's predictions to be verified. Sexually reproducing animals should be introduced as well.

Although highly simplified, we have shown how a costly behavior without any obvious value can evolve. We recognize that this could apply to nonfunctional behaviors of any type, and our labeling this behavior as play may seem a sleight of hand. But play has been used as the prime example of a mysterious, non-serious, energetic behavior perplexing scientists as to how it could originate and become fixed in a population unless it had, *at the same time* considerable value balancing its costs. Indeed, the ratio of costs to benefits has been an enduring and crucial parameter in behavioral ecology and evolution. We have shown that behavior can initially evolve in the absence of adaptive value. But once present, play, if it can result in expanding the resources available (e.g., invading new habitats, creating novel ways of exploiting resources), may become the avenue for further evolution, an idea supported elsewhere (Burghardt, 2015). But also, once present, resource enhancement occurring for other reasons (e.g., invasive food resource) may facilitate the extent and amount of play while contraction of resources (e.g., due to

climate change) may reduce it. Future model developments identifying the conditions in which the evolutionary processes underlying play are now needed.

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341 Table 1. Parameter descriptions for the model.

Parameter	Description	Values
t	Time	1, ..., T
T	Reproductive period (life cycle)	50, 100 , 1000
N	Population size	50, 100
α	Hunger threshold	Emerges from the model
$\rho(0)$	Initial amount of resources	25, 50 , 100
$\rho(t)$	Resources at time t	0, ..., $\rho(0)$
$E_i(0)$	Initial individual energy level	0.25, 0.5 , 0.75
β	Foraging ability	0.25, 0.5 , 0.75
κ	Energy benefit from successful foraging	0.25, 0.5 , 0.75
c	Resting energy cost	0.001, 0.01 , 0.1
ϕ	Unsuccessful foraging energy cost	0.1, 0.25, 0.5
ψ	Probability of dying when resting	0.0001, 0.001 , 0.01
η	Probability of dying when foraging (multiply with resting mortality)	2, 5 , 10
π	Individual time spent playing instead of resting	Emerges from the model
λ	Play energy cost	0.05, 0.1, 0.25
θ	Probability of dying when playing (multiply with resting mortality)	1, 2 , 5
γ	Play benefit scaling parameter	0* , 1 , 10
μ	Mutation rate	0.001
μ_e	Mutation effect	0.01
w_0	Baseline fitness	1
w_i	Individual fitness	Emerges from the model
s	Selection coefficient	0.1, 0.01 , 0.001

342 Values in bold were used for the simulations used in the results unless otherwise noted.

343 All combinations of parameter values were explored. (*) For the case when $\gamma = 0$ play

344 does not have a beneficial effect on foraging.

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Figure 2. Strategies and their payoffs for the player agents.

Figure 3. Dynamics of the play gene frequency and the play time. Figure (A) shows the

maintenance of a small amount of average time spent playing when not hungry

(~10%) in the population when there is no benefit to foraging success from play

behavior ($\gamma = 0$). The play gene becomes fixed in the population. Figure (B)

displays the rise and fall of play behavior in the population when there is a

foraging benefit associated with the amount of time an agent plays ($\gamma = 1$), yet

the play gene cannot be maintained and the population of players collapses.

Parameter values used are found in Table 1 and $\alpha = 0.5$.

Figure 4. The dependence of play behavior on resource abundance and other parameter

values. The vertical axis gives the average maximum play time in the population

(A) or average play gene frequency in the population (B) over the last 10000

generations and for 100 simulations. Outer axes correspond to different values in

the initial amount of resources for each generation ($\rho(0)$) and energy costs for

playing (λ), while inner axes correspond to different foraging ability (β) and play

benefit to foraging (γ). Simulations were run for 100000 generations and the other

parameter values used are given in Table 1.

Figure 5. The dynamics of resource abundance in the environment due to the amount of

play behavior in the population. For each simulation a proportion of the

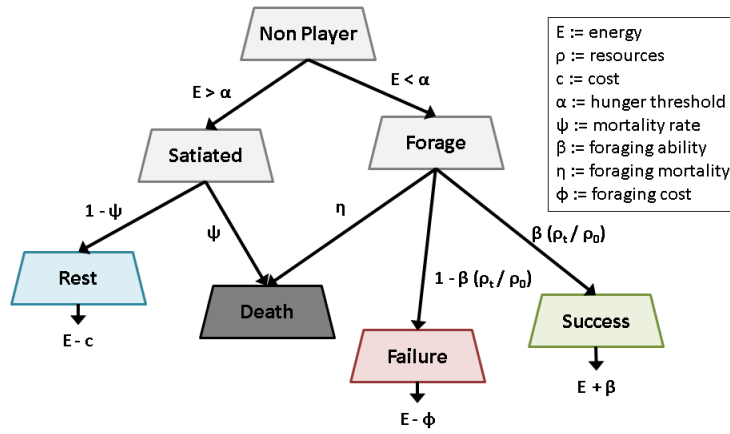
population were player agents with a fixed play time. Figure (A) shows the results

for the model without an increased foraging benefit from play behavior ($\gamma = 0$),

while (B) shows the results for the model with a play benefit to foraging ($\gamma = 1$). As play behavior becomes more frequent and play time increases it has a significant impact on the amount of available resources in the environment over the course of the individual's life cycle. Results were averaged over 100 simulations for each parameter combination (refer to table 1 for the other parameter values used in these simulations).

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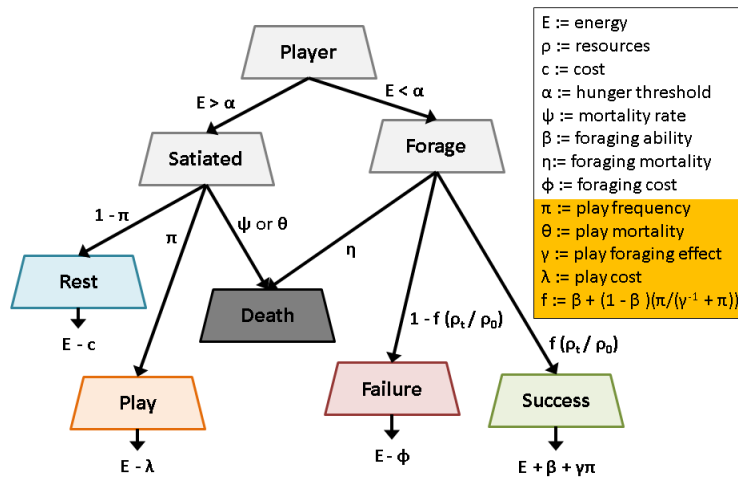
Figures



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Figure 2. Life history of the non-player agents.



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Figure 3. Life history of the player agents.

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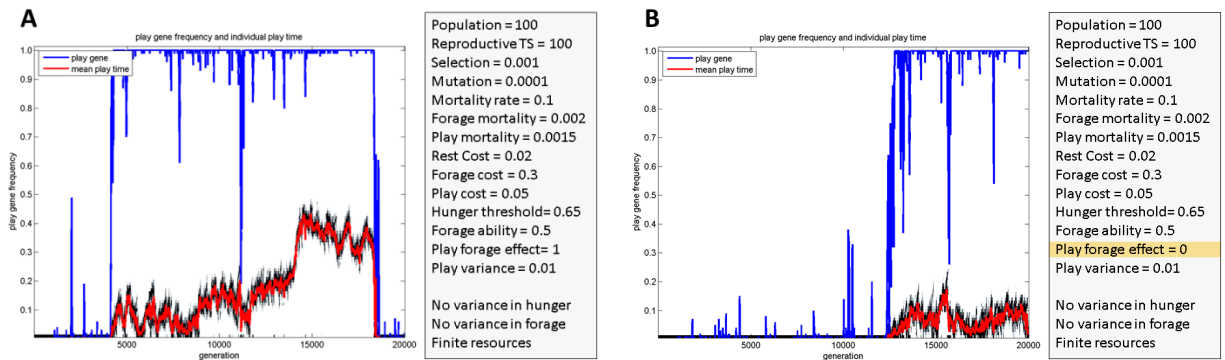


Figure 3. Plots of the play gene frequency and the play time in a population over 20000 generations for a given set of parameter values. Figure (A) displays the rise and fall of play behavior in the population when there is a foraging benefit associated with the amount of time an agent plays ($\gamma = 1$). This pattern repeats itself indefinitely when there is a increase to foraging success from playing. Figure (B) shows the maintenance of a small amount of average play time when not hungry ($\sim 10\%$) in the population when there is no increase to foraging success from play behavior. The play behavior is maintained indefinitely in the population at a low frequency.

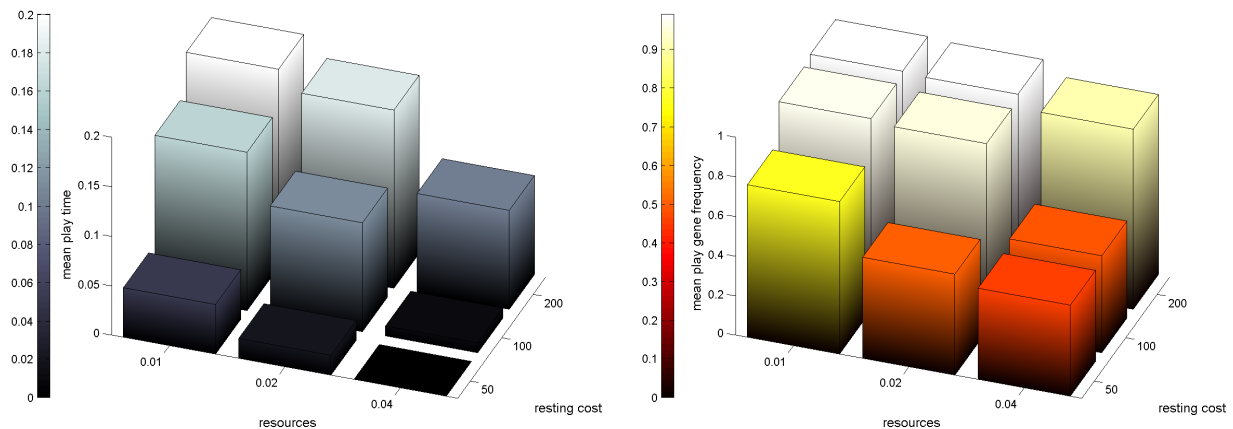


Figure 4. Plots of the play gene frequency and the play time averaged over 1000 populations during a period of 20000 generations for different parameter values. Figure (A) shows the mean play time for individuals in the population after play invades for different values of resting cost and initial amount of resources in the environment. Increasing costs to rest and decreasing the amount of resources

396 results in less time the organisms play. Figure (B) shows the mean proportion of
397 the population that carries the play gene. Decreased resources and increased cost
398 to resting reduced the play gene frequency but it was still maintained at > 40% of
399 the populations once it invaded.

400