THE EVOLUTION OF TWO TYPES OF PLAY

PAUL E. SMALDINO[1,*], ELISABETTA PALAGI[2], GORDON M. BURGHARDT[3],
AND SERGIO M. PELLIS[4]

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Lay Summary: Animals vary greatly in how much they play. Why? Some species do not appear to exhibit to play at all. Some exhibit only simple, often solitary, play behavior during juvenility, while others engage in complex, often social, play behavior that extends into adulthood. We discuss the evolutionary benefits and costs of play, review interspecies variation, and discuss how that variation relates to the evolutionary tradeoffs during life history. We structure our discussion around a simple mathematical model.

Abstract: Play is an important and understudied class of phenomena that likely serves a critical role in the ontogeny and maintenance of fitness-enhancing behaviors. Many species exhibit little or no play. Among those animals that do play, some exhibit only very simple forms, while others engage in complex play both solitarily and socially. Likewise, some animals play only as juveniles, while others continue to play as adults. We propose a general framework to explain inter-species variation in the evolution and emergence of simple vs. complex forms of play, supported by both a review of the empirical evidence and a novel mathematical model. The emergence of play requires that initial investment returns benefits that sufficiently compensate the opportunity costs associated with simple play. The subsequent evolution of complex play depends upon the interplay of several life history factors related to the benefits, costs, and time course of play investment. We conclude with implications for understanding the evolution of play across the animal kingdom.

Keywords: play, evolution, model, tradeoffs, development, social complexity

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[1]Department of Cognitive and Information Sciences, University of California, Merced, USA
[2]Department of Biology, University of Pisa, Italy
[3]Departments of Psychology and Ecology & Evolutionary Biology, University of Tennessee, USA
[4]Department of Neuroscience, University of Lethbridge, Canada
E-mail address: paul.smaldino@gmail.com.

1. Introduction

Many animals, including humans, play. Burghardt (2005) defines play as any behavior that meets all five of the following criteria: (1) it must have elements that do not contribute toward the organism's immediate survival; (2) it must be spontaneous or rewarding to the organism; (3) it must differ from strictly functional expressions of behavior either structurally or temporally; (4) it must be repeated in a similar form during at least a portion of the organism's ontogeny; and (5) it occurs when the organism is in a "relaxed field," meaning that it is healthy, sated, and not under stress from competing systems (e.g., feeding, mating, fear). However, behavior that meets the stringent criteria that enable it to be labelled as *play* is relatively rare in the animal kingdom, and emerges only sporadically in the phylogenetic tree of animals (Burghardt, 2005). Such a sporadic distribution suggests that play has evolved independently multiple times and that the conditions enabling it to evolve rarely coalesce.

Animals vary greatly in how much they play. Why? The adaptive benefit of play appears to stem from its characterization as a form of exploratory learning or as training for the unexpected (Spinka et al., 2001). Gopnik et al. (2015) have suggested that play serves as a time for broader search in the space of possible actions and outcomes, drawing an analogy between playful exploration and *simulated annealing*, the computational optimization algorithm in which random movements in solution space are initially frequent and grow rarer over time as the program classifies the regions leading to larger payoffs. Illustrating this functional role, Cully et al. (2015) studied six-legged robots who spent a "developmental" period engaging in self-handicapping in which they learned to move effectively while restricting certain aspects of their anatomy. They found that robots who engaged in this "playful" behavior were much better able to adapt to real injuries later on. The survival benefits of this sort of simple exploratory play are relatively easy to perceive. Such behaviors could evolve as long as those benefits outweigh the costs—in

terms of opportunity costs, predation risks, etc.—which may be substantial. Play involving more complex cognitive processing, particularly social play, may produce benefits that are less immediately realized. A common explanation is that the benefits to social play, such as the rough-and-tumble play observed in many mammals, come from learning specific social skills as juveniles that will be useful during adulthood (Pellis & Pellis, 2009; Pellis et al., 2010). Relatedly, Ciani et al. (2012) have proposed that in species where social play persists into adulthood, social play serves to continually reassess social relationships, particularly in social species without rigid dominance hierarchies. However, complex forms of play, including but not limited to social play, are relatively rare compared with simpler play behaviors, even among species with comparable cognitive abilities (Burghardt, 2005; Pelletier et al., 2017). Such behaviors incur costs that equal or exceed the costs of simpler play, and may require more time or social investment to yield any benefits they may confer.

Throughout this paper we will refer to play as "simple" when it requires relatively little costly investment. Such play will often be solitary and involve simple exploration of physical or behavioral space. We will refer to play as "complex" when it requires a substantial investment of cognitive and/or temporal resources, as when monkeys close their eyes during locomotor play (Kavanagh, 1978) or rodents keep track of their partner's movements and disposition in rough-and-tumble play (Pellis et al., 2010). In reality, play of intermediate complexity exists, but we restrict our focus to this binary distinction for the sake of clarity. What, then, explains the variation in the complexity of play behaviors among species that play? We propose that a focus on the costs and benefits of play in terms of the resources invested in play behavior provide a much needed lens through which to consider the evolution of play. We will explore how such a lens can help to explain the interspecific distribution of complexity in play behaviors.

Theoretical considerations (Burghardt, 2005) and formal models (Auerbach et al., 2015) suggest that, at its inception, play can emerge with little or no fitness payoff. Once

present, play can be co-opted for novel functions, but this requires the development of new cognitive or physiological control mechanisms and the expenditure of more time and energy to perform new variations and repetitions of the modified play behavior (Pellis et al., 2015). Further transformations in the organization and frequency of play can be added as new and more varied benefits are gained by playing (Pellis et al., 2014). Such a transformation process is likely to be costly, and the complexity of evolved play may vary with the net costs incurred by playing. This is suggested by a phylogenetic analysis of social play in murid (mouse-like) rodents. Across a range of species, play can be absent or present. If present, play can show different degrees of complexity, from the simple approach and withdrawal of house mice to the wrestling of rats and Syrian hamsters. Intermediate levels of complexity in the play performed are also present in other species (Pellis & Pellis, 1998). Mapping this complexity on a cladogram reveals that at the base of the tree the ancestral condition is likely to be one of moderate complexity, but some lineages may have increased that complexity further. Most striking is that there are also losses, so that in some lineages there is reduced complexity or even the elimination of most play altogether (Pellis & Iwaniuk, 1999). Although traits can be lost through drift, such loss is unlikely to be common if a trait confers a consistent benefit. The loss of play strongly suggests that there is a high cost associated with maintaining play, especially in its most complex forms. That is, if the benefit from investing in play is diminished, the cost of maintaining play can no longer be supported.

This pattern, of play emerging sporadically and only evolving to high levels of complexity in rare cases, has been documented repeatedly across several lineages of mammals, such as rodents and primates (Palagi, 2018; Pellis & Pellis, 2009) and for some lineages of birds (Diamond & Bond, 2003). Moreover, in the case of rodents we have learned much about the underlying neural and psychological mechanisms that enable play to be produced and regulated (Siviy, 2016; Vanderschuren et al., 2016), and have also gained some idea of how these mechanisms can be modified to yield more complex forms of play

(Pellis & Pellis, 2016). There is evidence that the experience of more complex forms of play—such as play fighting, which requires negotiating and maintaining reciprocal exchanges (Pellis et al., 2017)—can lead to refined socio-cognitive skills and to changes in the neural machinery underlying such skills (Pellis et al., 2014; Vanderschuren & Trezza, 2014). Simpler forms of play, such as play that emphasizes locomotor-rotational movements, may function to facilitate the development of neuromuscular systems and predator-avoidance responses (Byers & Walker, 1995). However, in order to influence the development of sophisticated processes (such as socio-cognitive systems), animals need to engage in more complex social play (Pellis et al., 2010). Indeed, even within the same species, simpler locomotor play improves motor function (Nunes et al., 2004) but fails to improve socio-cognitive skills, which *can* be modified by social play (Marks et al., 2017). Some complex play behaviors may also require advanced cognitive machinery, such as bigger brains, to emerge at all. Bigger brains have well-known caloric and developmental costs. In the case of humans, who have the biggest brains and are the most social and playful of the primates, intense sociality and adaptive social learning likely coevolved with the bigger brains that support those behaviors (Muthukrishna & Henrich, 2016; Muthukrishna et al., 2018). Much adaptive social learning, especially during childhood, occurs in the form of playful interaction.

Simpler forms of play are more widespread than more complex forms of play (Burghardt, 2005; Fagen, 1981), require fewer resources to maintain, and yield less generalizable benefits. This implies that gaining a net benefit for simpler forms of play should be more readily achievable than gaining a net benefit for more complex forms of play. Indeed, casual observation reveals that immature animals from species that have to sustain more of their own individual survival costs (e.g., obtain their food, find their own shelter, avoid predators) tend to engage in simpler forms of play (or no play at all) compared with species for which parents provide much of their food, shelter, and protection against

predators (Burghardt, 1988). The latter are likely to engage in more play and in particular more complex forms of play. That is, more precocial species engage in more simple play than complex play and more altricial species engage in more complex play than simple play (Fagen, 1981; Ortega & Bekoff, 1987). The precocial-altricial distinction is, of course, more nuanced than implied by this binary labeling. Comparisons across species reveal differences in degree. For example, house mice gain sexual maturity sooner in their lifecycle than do rats, and mice have a simpler form of social play that emphasizes locomotion (Pellis & Pasztor, 1999). Rats engage in locomotor play as well (Pellis & Pellis, 1983), but also engage in more complex playful wrestling (Pellis & Pellis, 1987). Using a graded scale for comparison, several studies on several animal lineages have shown that engaging in more complex forms of play is positively correlated with an increased period of immaturity (Diamond & Bond, 2003; Pellis & Iwaniuk, 2000b).

Thus, the variation in play across the animal kingdom is well documented, and some of the variation in the relative presence of simpler versus complex forms of play is known to be linked to lifestyles that change the relative costs of playing (Burghardt, 2005; Fagen, 1981). Nevertheless, a general theory explaining that variation is lacking. In this paper, we take steps toward filling that gap. Our verbal theory works as follows. Organisms can make costly investment in play behavior, representing the time and energy resources the organism commits to play at the expense of other behaviors, such as foraging, predator avoidance. Investment could also include delayed time to sexual maturity to provide more time for play, in which case the associated cost would be the potential decrease in fecundity. Such investment in play may yield benefits to fitness, via learning and establishment of social relationships. Simple play is characterized by positive returns to fitness for relatively little investment, but also by a low ceiling on the maximum possible benefit. In contrast, complex play is characterized by requiring more substantial investment in order to yield benefits to fitness, but also by the potential of greater benefits if the investment can be made. Thus, we propose that interspecies differences

in the complexity of play behavior can be explained to a large extent by differences in the cost of investing in those behaviors, as well as by the extent to which complex play requires more investment and yields a higher potential benefit.

In the next section, we formalize and refine this argument with a simple mathematical model. Mathematical and agent-based computer models have begun to identify the conditions that can sustain play and lead to the evolutionary spread of play when it is associated with an advantage (e.g., Cenni & Fawcett, 2018; Dugatkin & Bekoff, 2003; Durand & Schank, 2015; Schank et al., 2018; Grunloh & Mangel, 2015). As the empirical data are sparse and diverse, a model that can identify the relevant trade-offs can be invaluable in directing empirical research. All of the aforementioned models focus on the evolutionary role of one specific type of play and not on the transitions between different play types. Our work builds on this foundation to explore the conditions that enable animals to switch from engaging in simpler to more complex patterns of play. We ask: what are the evolutionary drivers that promote the evolution of more complex play?

2. Model and Analysis

Consider selection on the amount of resources an organism invests in play. This investment can be represented by the proportion, x, of total available developmental time and energy resources the organism commits to play at the expense of other behaviors, such as foraging, predator detection, or mating once sexually mature. We do not explicitly model any social interaction or life history in this model, only the resources individuals can invest in play behavior. That said, we conceptualize x as the total investment in play during development rather than a discrete, immediately invested resource.

In addition to the investment trait x, individuals also express a play strategy: complex play, simple play, or no play. No play yields no benefits, but also requires no investment. Each of the two positive play strategies yields a benefit that increases monotonically

with x. We incorporate the two key properties of play mentioned above into our benefit functions. First, play requires some minimum investment before yielding substantial fitness benefit, with complex play requiring more investment than simple play. Second, past some (potentially soft) threshold, additional investment in play fails to yield significant marginal benefit. These two constraints are well captured by a sigmoid function (Figure 1A). Specifically, we define the benefit of simple play as

$$(1) \qquad B_s(x) = \frac{1}{1 + e^{-\gamma(x-\alpha)}},$$

where γ is the rate at which the initial benefits of play manifest relative to investment, and α is an offset indicating the investment that corresponds to half the maximum possible benefit. We parameterize the function so that the benefits of simple play begin to increase with very low initial investment. Our analyses indicate that the exact values of these parameters are not particularly important, and so for all of our results we used $\gamma = 20$ and $\alpha = 0.2$. For the reader interested in further exploration of our model, we provide the Mathematica notebook used to generate all of our figures as a Supplement.

Complex play is characterized by the requirement of greater investment to achieve initial benefits, but also by a larger maximum possible benefit. Specifically, we model the benefit of complex play as

$$(2) \qquad B_c(x) = \frac{b}{1 + e^{-\gamma(x-\alpha-\delta)}},$$

where δ is the additional investment required for benefits to manifest and $b > 1$ is the maximum achievable benefit. In other words, the difference between simple and complex play is fully described by the additional investment required for complex play and by the additional benefit that can be realized through such an investment. Whether simple or complex play evolves is determined by how the benefits from investing in play relate to the costs of that investment.
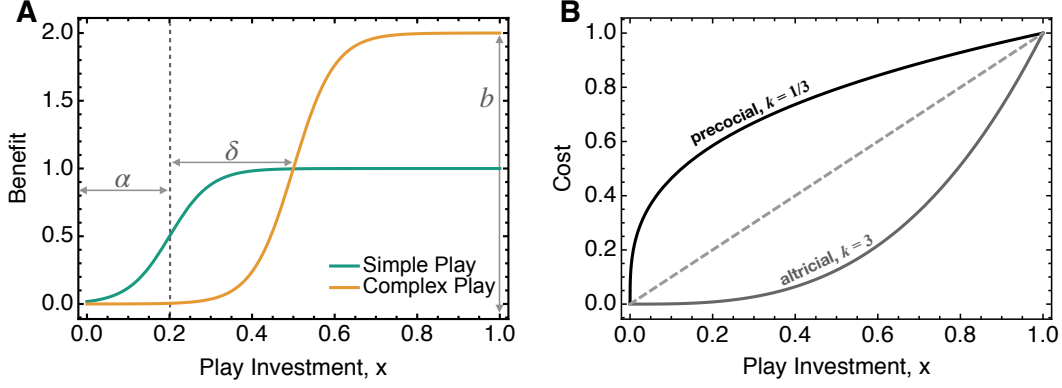
FIGURE 1. Model assumptions. (A) Relative to simple play, complex play requires additional investment, δ, for benefits to become substantial, but also has maximum benefits that are increased by a factor b. (B) The cost of play increases with investment, but the initial increase can either be slow, as with altricial species, or fast, as with precocial species.

Investment in play incurs costs. We focus on the opportunity costs of playing that come from the loss of investment into other fitness-enhancing activities, such as foraging, eating, or watching for predators. In addition, there may be energetic costs directly associated with specific play behaviors, which may differ for simple and complex play behaviors; as mentioned, complex play may carry the metabolic costs of larger brains or the physical risks from angering a conspecific. For simplicity we ignore these behavior-specific costs, and model the cost as a monotonic function of investment in play. That said, the curvature of this function may be related to the life history of an organism. For example, an altricial species receiving extended parental care may have ample time to invest in play because its other needs are met by its parents, and thus the cost of small investments in play could be low. In contrast, a precocial species might need to devote most of its energy to basic survival needs, so that even a little investment in play could be very costly. To capture this variation, we model the cost of investment in play using a simple power function,

$$(3) \qquad\qquad C(x) = x^k.$$

In the above example, smaller k represents the more precocial case and larger k represents the more altricial case (Figure 1B). Here we use the words "altricial" and "precocial" rhetorically, with the former term simply indicating those species who can afford more investment or a longer period of vulnerability during development compared to the latter; we do not define a strict cutoff between these two categories. We certainly do not wish to suggest that organisms born precocial never play, as there is ample evidence that many of them do (Burghardt, 2005).

The evolution of play then depends on the net benefit,

$$(4) \qquad W_i(x) = B_i(x) - C(x),$$

where $i \in \{n, s, c\}$ indicates the type of play or lack thereof: no play, simple play, and complex play, respectively. This net benefit is the fitness contribution to the organism from investing in play. Our analysis relies on adaptive dynamics. We begin by considering a monomorphic population of organisms with investment $x \approx 0$ and play strategy $s = n$; in other words, a species that does not play. We then consider whether a mutant with an incrementally larger investment x' using any play strategy could invade and spread to fixation. This is repeated until an incremental increase in play investment fails to yield a positive marginal benefit, at which point we examine which play strategy is dominant.

This simple model can help us understand what types of play, if any, we should expect to evolve given an organism's life history. If the initial cost of investing in play is greater than the marginal benefit of initial investment, we should expect play to be rare or nonexistent. This will occur whenever $\frac{\partial W_s(\epsilon)}{\partial x} < 0$, where ϵ is a vanishingly small positive real number. If the net benefit of initial investment in (simple) play is positive, simple play will evolve. Investment in play will increase until the marginal benefit of further investment vanishes, that is until $\frac{\partial W_s}{\partial x} = 0$. We calculate the rate of change of the net

benefit from simple play to be

$$(5) \qquad \frac{\partial W_s}{\partial x} = \frac{\gamma e^{-\gamma(x-\alpha)}}{\left[1 + e^{-\gamma(x-\alpha)}\right]^2} - kx^{k-1}.$$

If this derivative reaches zero before the net benefit of complex play surpasses the net benefit of simple play, then complex play will not evolve, because the organism will not benefit from any incremental increase in play investment. If, on the other hand, the net benefit of complex play surpasses the net benefit of simple play with investment below the threshold where $\frac{\partial W_s}{\partial x} = 0$, complex play will evolve. The three possible evolutionary trajectories of play discussed here are illustrated in Figure 2. For a wider range of parameter values, equilibrium play strategies were calculated using numerical simulation, the algorithmic details of which can be found in the Mathematica notebook that accompanies this paper as a Supplement.

Our analysis of the model yields three broad conclusions. First, if the marginal cost of initial investment in play is too high, play cannot evolve. Indeed, this may help explain why play is absent in so many animals, especially those without endothermy (which facilitates extended bouts of vigorous activity) and parental care (which buffers juveniles from sustaining costs of foraging, predator vigilance, and thermoregulation). Under our formalization, the evolution of play requires a developmental period in which the initial cost of play investment is outweighed by the initial benefit. For many animals, the initial benefits of play may accrue slowly or rapidly, but there is likely to be at least some delay in their accrual relative to the initial investment. If that initial investment in play corresponds to a negative net benefit, no play will evolve. In reality, this corresponds to the case where investment in play decreases overall fitness, such as by exposing an organism to likely predation, in which case selection should inhibit the evolution of all but the simplest and most immediately beneficial play behaviors. If, on the other hand, the cost of investing in play increases more slowly, various forms of play can evolve.
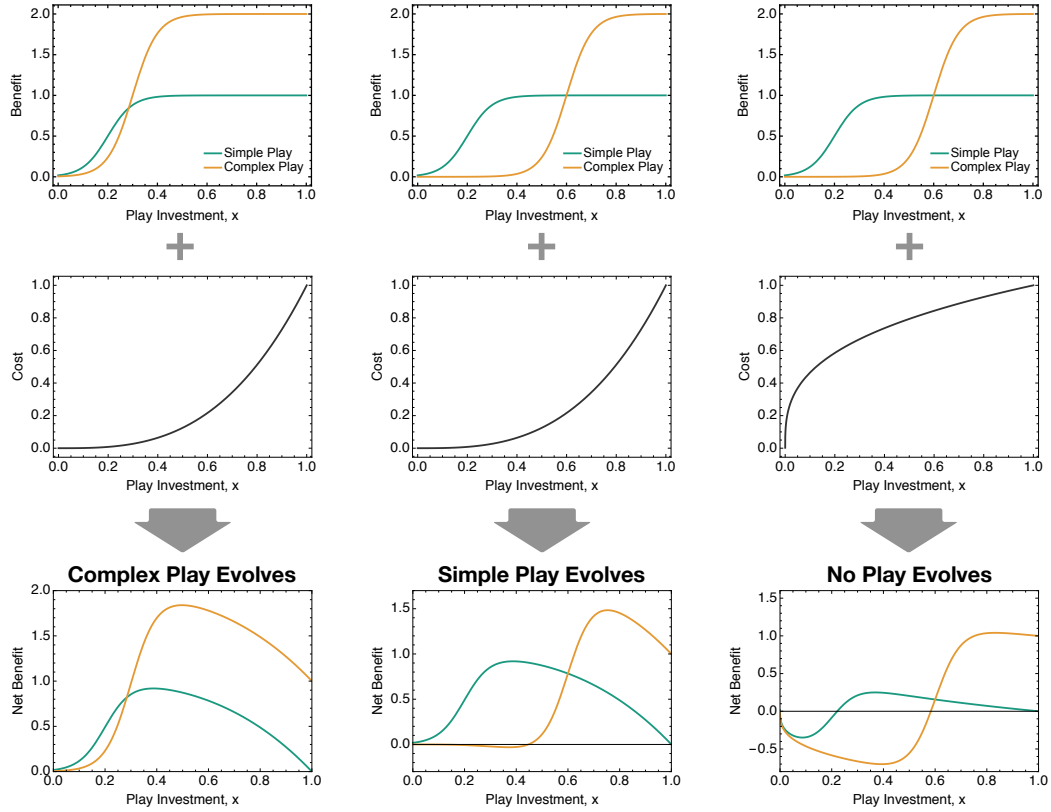
FIGURE 2. The dynamics of play. Left: If the benefit of complex play manifests with little more investment than simple play and the costs of early investment increase slowly, the net benefit of play will yield the eventual adoption of complex play behavior. Middle: If the benefit of complex play takes more investment to manifest, the marginal benefit of increased investment in play may decrease before complex play is favored, leading to the evolution of simple play only. Right: If the costs of early investment in play increase rapidly, the net benefit of low levels of play can be negative, foreclosing the evolution of any play at all.

Second, both simple and complex varieties of play can evolve as long as the costs of play do not increase too rapidly with initial investment. That is, play can evolve if organisms are sufficiently "altricial" (k is sufficiently large). This is illustrated in Figure 3. The evolution of complex play typically relies on the prior evolution of simple play. Whether simple play eventually leads to complex play during the organism's development or evolution depends instead on the characteristics of the complex play behaviors
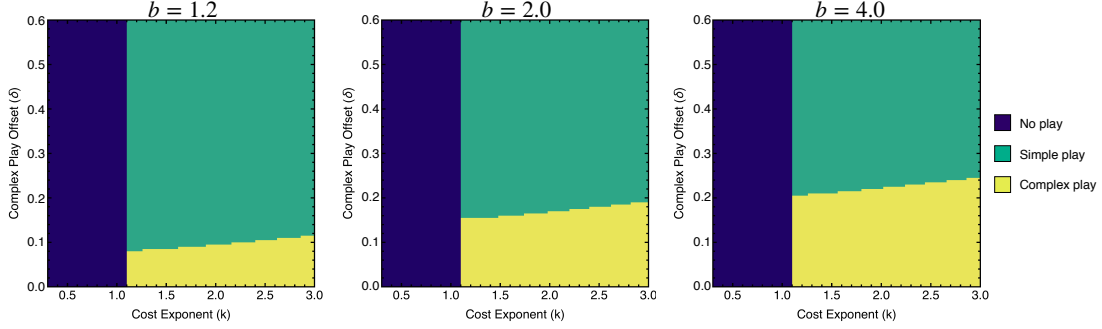
FIGURE 3. The evolution of two types of play. Higher values of the cost exponent, k, indicate costs that increase more slowly with investment (as in more altricial species), while higher values of the complex play offset, δ, indicate a larger investment in complex play needed to manifest its benefit. Dark blue regions represent parameter combinations that prohibit the evolution of play of either type. Parameter combinations that lead to the evolution of simple and complex play are shown in green and yellow, respectively. For these analyses $\gamma = 20$ and $\alpha = 0.2$.
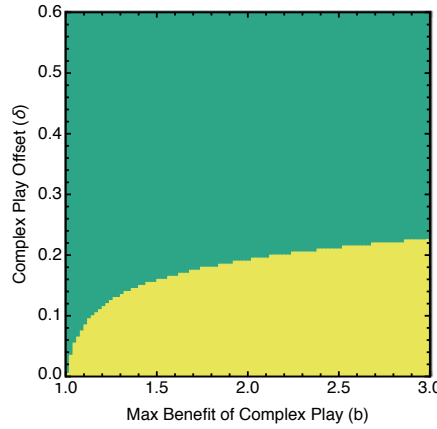

FIGURE 4. The evolution of complex play (yellow region) is favored when the maximum benefit of complex play (b) is high and when the additional investment needed to manifest that benefit (δ) is low. Here $k = 3$, $\gamma = 20$ and $\alpha = 0.2$.

themselves. That said, the evolution of complex play is favored under a wider range of conditions as the slope of the cost function becomes shallower (Figure 3).

Third, the evolution of complex play is favored when the additional investment required for its benefits to manifest is minimized. The more investment required to realize

the benefits of complex play, the less likely it will evolve. However, this limitation can be overcome to some degree if the benefits of complex play are large relative to those of simple play (Figures 3 and 4).

3. Discussion

Our formal model is very simple, and serves primarily to codify a rather straightforward consideration of costs and benefits. Nevertheless, we believe that our analysis helps to clarify and structure a number of empirical findings about the evolution of play, for which until now such structure has been lacking.

A major problem in comparing the relative benefits of simple and complex play is in how to evaluate their relative costs. For example, simple locomotor play may be limited to short, brisk runs, whereas complex locomotor play may include head-shaking and rapid whole-body rotation as well as the runs, yet an animal limited to the simple form may spend as much time engaged in locomotor play as an animal capable of the more complex form. Consequently, from an energetic perspective, it may not be the *prima facie* case that complex play is more costly than simple play. However, where comparative data are available, it does seem to be the case that there are lower relative costs for more simple forms of play compared to more complex forms. In murid rodents, locomotor play may be absent, be limited to brief bursts of running, or involve complex sequences of runs, jumps and rotations, with those engaging in more complex forms performing such play more often (Pellis & Iwaniuk, 2004). Similarly, rodents with more complex forms of social play also engage in such play more often (Nahallage & Huffman, 2007; Pellis et al., 1989). Species of macaques that exhibit a wider variety of object play behaviors also spend more time engaging in those behaviors (Pelletier et al., 2017). Comparatively, then, it is likely that species that engage in more complex forms of play also tend to play more, making complex play more energetically expensive. There are also other kinds of costs associated with complex play.

Developmentally, whether object, social or locomotor play, the early versions to emerge are simpler (Pellis & Pellis, 1983; Nahallage & Huffman, 2007; Cordoni & Palagi, 2011). This suggests that it requires greater sensorimotor capacity to sustain more complex forms of play, a level of control that may involve both greater muscle and brain control over bodily movements (Byers & Walker, 1995). Moreover, with regard to social play, it is known that the regulatory mechanisms needed to motivate, execute and sustain play fighting in rats do not require the cortex (Siviy, 2016; Vanderschuren et al., 2016). However, to be able to adaptively modify that play to deal with contextual factors, such as the identity of the partner, neural circuits involving the cortex are needed (Pellis & Pellis, 2016). That is, more complex forms of social play require the engagement in more neural circuits. Together, these studies suggest that more complex play may be more energetically expensive than simpler forms of play, and may also include other hidden costs, such as added sensorimotor and neural demands. With regard to our model, these considerations make the assumption that complex play has higher relative costs than simple play reasonable as a starting point to tackle the unexplored problem of the evolutionary relationship between simple and complex forms of play.

The opportunity cost of initial investment in play may be very high, as in the case of many solitary precocial animals, or it may be low, as in the case of many altricial species receiving extended parental care. For play to evolve, the cost of initial investment in play must not exceed the benefit of that investment. Our model predicts that as the initial cost of investing in play is lowered, a threshold will separate conditions that do or do not favor the emergence of simple play. In particular, the division between no play and some play is driven entirely by the initial opportunity cost of investing in play, which cannot increase faster than the initial marginal benefit of play. If the cost of initial investment of play is sufficiently low, either simple or complex play can evolve. The evolution of complex play is favored by further decreases to the opportunity cost of investment, decreases to the amount of added investment needed to manifest the benefits

of complex play, and increases to the relative amount of benefit achieved by sufficient investment in complex play. The divide between the cost functions that prohibit or allow the evolution of play may explain the secondary loss of play observed in the cladograms of some lineages (Pellis & Iwaniuk, 1999, 2000a), and it may be possible to characterize this loss in terms of differential costs or risks during early ontogeny. Note also that with the advent of extensive parental care, selection is likely relaxed on maintaining the often elaborate and refined innate behavior systems employed by neonates and hatchlings to fend for themselves. Play may be a means of maintaining, through exercise and practice, abilities animals needed to possess early in ontogeny before the advent of altriciality and parental care (Burghardt, 1984, 1988).

Our model helps to facilitate how we think about these transitions: from no play to simple play, and from simple play to complex play. While we have discussed the involvement of more locomotor elements and less social contact as a demarcation between simple play and complex play, it should be noted that even locomotor play can vary markedly in complexity, ranging from simple runs, to the runs with hops and rotations of mice (Walker & Byers, 1991), to the pirouettes of bonobos and chimpanzees (Nishida & Inaba, 2009; Palagi, 2008; Palagi & Cordoni, 2012). Similarly, playing with objects can vary markedly in complexity, even among closely related species (Pelletier et al., 2017). Whatever the particular form of play studied, the present model would suggest that simpler forms would be more readily evolved than more complex forms because the threshold investment level at which a net benefit is gained would be easier to achieve. The distribution of play in the animal kingdom (Burghardt, 2005; Fagen, 1981) is consistent with this expectation. Nevertheless, our empirical knowledge is incomplete. In general, we know more about the functions of more complex forms of social play than about the functions of simpler forms of play. It will therefore be helpful to highlight several empirical cases for which our model can help clarify the transition from simple to complex play. Less is known about the transition from no play to simple play. We

hope our analysis will inspire researchers to bolster the empirical data to evaluate this transition. Where possible, we make specific predictions that could be tested empirically.

Rodents. Social play (play fighting) in murid rodents can range in complexity from simple approach and withdrawal to very complex and sustained wrestling (Pellis & Pellis, 1998). Although not empirically tested in all relevant species, it appears that some complex play has a benefit for improving the behavioral actions being 'simulated' for adult functional contexts (e.g., mounting during sexual encounters is improved by playful mounting in the juvenile period; Moore, 1985; Nunes et al., 2004). However, not all murid rodents gain socio-cognitive benefits from complex play (Einon et al., 1981), suggesting that only those species capable of the requisite investment in play gain this more sophisticated benefit (e.g., rats, Syrian hamsters; Baarendse et al., 2014; Bell et al., 2010; Burleson et al., 2016). If so, future research should observe a threshold effect for engaging in those particular play tactics. That is, we may observe that all rodent species who engage in complex play invest in play behavior *at least* some threshold amount, with little to no complex play in species who are unable to invest in this level of play.

For social play to remain playful, some degree of turn taking is necessary (Cordoni et al., 2016; Palagi et al., 2016b; Pellis & Pellis, 2017), and this requires tapping into socio-cognitive skills in a way that is adaptable to changing contexts (e.g., novel partners, novel actions by partners; Pellis & Pellis, 2016). In some species, such as rats (Foroud & Pellis, 2002), this turn taking has been shown to be exaggerated at the age when the training of these skills is of maximum benefit (i.e., when the underlying neural systems are developing and most plastic; Arakawa, 2017). Diminishing the experience of play containing such turn taking, either by blocking playful physical contact altogether or by providing inhibited partners that support fewer opportunities for playful turn taking, alters neural development and impoverishes associated socio-cognitive skills (e.g., Baarendse et al., 2014; Van Kerkhof et al., 2013; Pellis et al., 2017; Schneider et al.,

2016a,b). If this is a general phenomenon, and it is consistent with the model in showing a steep rise needed in play investment to gain the benefit from complex play, then we predict that only those species that gain the net benefit from complex play in terms of socio-cognitive development should exhibit this increased turn taking in the peak juvenile period, and perhaps even that only these should exhibit the neurophysiological structures associated with those play behaviors.

An alternative way to consider this issue is that the benefits of complex social play are characterized by a net gain in socio-cognitive skills. The conditions favoring such play are likely to be met only in those species for which enhanced socio-cognitive skills as adults has a sufficient pay-off to warrant the investment in play earlier in life. A limiting factor in achieving this net gain is therefore the value of this increased capacity in adults. One of the most intensively studied mammalian lineages that would be amenable to a comparative test of the model-derived hypothesis is the primates. For this taxon, more than any other, there are many studies on play (Cordoni et al., 2018; Palagi, 2018) and a rich data set on a variety of natural history traits (Campbell et al., 2010).

Primates. In a comparative study of juvenile play across primates, our analysis suggests we should find a steep or stepwise increase in the frequency and/or elaboration of tactics that promote an increase in turn taking, following from our discussion of the evolution of similar behaviors in rodents. Further, only those species able to *benefit* from such increased socio-cognitive skills as adults should show this increase. The beauty of this framing is that the prediction forces us to look beyond superficial differences in what may constitute play complexity and to focus only on those complexities that are essential to facilitating improvements in socio-cognitive skills (Cordoni & Palagi, 2011). This is an important distinction that is often muddled in the current literature. There may be many ways in which different aspects of play become more or less complex in different species. For example, the great apes can clearly engage in very complex actions

during play, and do so with greater frequency than many other primates (e.g., lowland gorillas, Palagi et al., 2007; bonobos, Palagi & Paoli, 2007; chimpanzees, Palagi & Paoli, 2007). As an illustration, some species of Old World monkeys have been reported to close their eyes when engaging in both locomotor and social play, increasing the riskiness of the behavior and the cognitive demands on the actions (e.g., Kavanagh, 1978). However, direct comparisons between Japanese macaques and orangutans has shown that while both species engage in such eye closing during play, orangutans do it much more frequently (Russon & Vasey, 2012). The clade encompassing the great apes has an expanded frontal cortex that is associated with greater socio-cognitive skills (e.g., Semendeferi et al., 2001). Thus, in this case, phylogeny of ape species may be most influential in accounting for these species differences.

Models such as ours, because they require more precisely defined assumptions (Smaldino, 2017), can be instrumental in drawing attention to specific features of the phenomena in question and so stimulate more focused empirical tests of the presumed relevant relationships. If a comparative test like the one described above were to reveal a steep curve in the incidence of turn-taking tactics at around the point when the benefits of increased socio-cognitive skills reach the relevant cost-benefit threshold, it would lay the foundation for extending the model and empirical testing a step further.

Retention of play into adulthood. Some species retain various forms of play into adulthood (Palagi, 2011; Palagi et al., 2016a), with social play being the most intensively studied (Pellis, 2002). Detailed studies of adult-adult playful interactions in several species suggest that individuals use play as a tool to solve a variety of social problems, including negotiating dominance relationships, maintaining friendships, de-escalating social tension, and fostering cooperation (Antonacci et al., 2010; Ciani et al., 2012; Norscia & Palagi, 2011; Palagi, 2006; Pellis et al., 1993). While many ecological and social factors may contribute to the retention of such play in adulthood (O'Meara et al., 2015), a key

feature that is strongly correlated with its retention is a social system based on fluid relationships which introduce uncertainty among the groupmates (Pellis & Iwaniuk, 1999, 2000a). This correlation has been reinforced by many detailed studies (Palagi, 2011; Palagi et al., 2016a; Scopa & Palagi, 2016). Critically, studies of juvenile play in those species that engage in adult play have shown, relative to members of the same genus that do not engage in adult play, that juveniles increase the occurrence of turn-taking and other actions likely to involve greater socio-cognitive skills and emotional regulation (e.g., Palagi et al., 2018; Petit et al., 2008; Reinhart et al., 2010). This suggests that for some animals, their social systems demand more refined socio-cognitive skills to be successfully navigated, and these skills are achieved by modifying the content of play in the juvenile period. In social groups with relationships codified according to rank-rules, formal dominance displays are sufficient to maintain social homeostasis. In species with more subtly nuanced relationships, however, the retention of play in adulthood may provide a tool for greater degrees of social assessment and manipulation than is afforded by simpler dominance displays (Pellis & Pellis, 2009). Indeed, the steepness of the dominance hierarchy curve—a measure of hierarchy similar to a Gini curve, in which steeper curves indicate more unequal distributions of power—is lower in species that play as adults, indicating greater ambiguity in social relationships (Ciani et al., 2012; Cordoni & Palagi, 2016; Palagi, 2015; Palagi & Demuru, 2017).

The present model could be extended, so that what is here relegated as 'simple play' could be re-labeled as 'juvenile play only' and what is relegated here as 'complex play' could be re-labeled as 'juvenile + adult play.' Again, we would predict that the latter would have a steeper climb to reach a net benefit. Macaques could be particularly useful for testing this prediction (Thierry, 2007). At the extremes, despotic species, having less social ambiguity, do not appear to exhibit adult-adult play, whereas egalitarian species, experiencing greater social ambiguity, do (Ciani et al., 2012; Scopa & Palagi, 2016). There are also species in between these extremes that have not yet been studied with

regard to play. It is predicted that as unpredictability of social interactions increase from despotic to egalitarian, there should be a threshold at which the gain in playing offsets the costs of playing. Thus, rather than expecting a smooth change along this dimension in terms of adult play (i.e., a small amount of play gives some benefit, more play provides greater benefit), it is predicted that there will be a sharp increase at some point along that dimension where the threshold benefit is obtained.

The idea that egalitarianism is associated with increased utility of adult play is further reinforced by some indications from the human literature that more egalitarian societies also exhibit more adult play, as well as more play in children (Gray, 2009; Burghardt, 2013; Palagi et al., 2016b). More generally, many have proposed that that our sociality and attentiveness to norms requires us to learn extensively the schemas and social roles of our culture (Dunbar, 2009; Muthukrishna & Henrich, 2016). The evolution of complex play in the human lineage may have played an important part in this learning.

Conclusions. There are still few models of the evolution of play, and ours is, to our knowledge, the first to consider the tradeoffs between more than one type of play. As such, it is necessarily simple. Future work should consider the consequences of incorporating additional complexity into our assumptions. We highlight a few examples. First, we used a binary categorization of play types, which is a very common type of simplifying assumption. However, variation in play behavior is likely to be more continuous in its complexity and multidimensional in its modality. How this additional complexity interacts with behavioral variation and socio-cognitive demands is an important question. Second, we did not consider the effect of behavior-specific costs for simple and complex play varieties. Complex play may incur additional costs that could further dampen its benefit to evolutionary fitness. Third, we assumed that complex play carries a constant fitness benefit for a given level of investment, independent of its frequency

in the population. We believe this is a reasonable assumption, and is in line with research documenting the heritability of individual differences in play behavior (Walker & Byers, 1991; Madrid et al., 2018). Nevertheless, the benefits of social play will often depend on the structure of one's social group and the distribution of phenotypes in that group. Traits that involve cooperative interactions often require additional considerations (Smaldino, 2014). Although our model's power derives from its simplicity, future work may incorporate the importance of cooperation for the evolution of complex play. In such cases, social play could potentially be modeled as a Stag Hunt game, in which non-participation is not exploitive, but where mechanisms for effective coordination are required to yield synergistic benefits (Calcott, 2008; Skyrms, 2004).

It is only recently that a precise definition of play was put forth, allowing for its rigorous scientific study across the animal kingdom (Burghardt, 2005). The difficulty in defining play is all the more reason that caution must be taken to be precise in characterizing play behaviors and in making predictions about the evolution of those behaviors. Although our model is simple, it nevertheless accounts for greater complexity than many of its predecessors, and we believe it provides an important scaffold for theorizing and organizing empirical results about the evolution of simple and complex play. In his defense of simple models, JBS Haldane (1964, p. 350) wrote, "In the consideration of evolution, a mathematical theory may be regarded as a kind of scaffolding within which a reasonably secure theory expressible in words may be built up. ...[W]ithout such a scaffolding verbal arguments are insecure." Our simple model provides a scaffold upon which richer theories of the evolution of play may be constructed.

Acknowledgments

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