



The co-evolution of juvenile play-fighting and adult competition

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The coevolution of juvenile play-fighting and adult competition

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Abstract

Although play-fighting is widespread among juvenile mammals, its adaptive significance remains unclear. It has been proposed that play is beneficial for developing skills to improve success in adult contests (motor training hypothesis), but the links between juvenile play-fighting and adult aggression are complex and not well understood. In this theoretical study, we investigate the coevolution between juvenile play-fighting and adult aggression using evolutionary computer simulations. We consider a simple life history with two sequential stages: a juvenile phase in which individuals play-fight with other juveniles to develop their fighting skills; and an adult phase in which individuals engage in potentially aggressive contests over access to resources and ultimately mating opportunities, leading to reproductive success. The simulations track genetic evolution in key traits affecting adult contests, such as the level of aggression, as well as juvenile investment in play-fighting, capturing the coevolutionary feedbacks between juvenile and adult decisions. We find that coevolution leads to one of two outcomes: a high-play, high-aggression situation with highly aggressive adult contests preceded by a prolonged period of juvenile play-fighting to improve fighting ability, or a low-play, low-aggression situation in which adult contests are resolved without fighting and there is minimal investment in play-fighting before individuals mature. Which of these outcomes is favoured depends

27 on the mortality costs and on the type of societal structure: societies with strong reproductive skew,
 28 favouring monopolisation of resources, show high levels of adult aggression and high investment in
 29 juvenile play-fighting, whereas societies with low reproductive skew have both low adult aggression
 30 and low levels of play-fighting. A review of empirical evidence, particularly in the primate genus
 31 *Macaca*, highlights some limitations of our model and suggests that other, complementary functional
 32 explanations are needed to account for the full range of competitive and cooperative forms of play-
 33 fighting. Our study illustrates the power of evolutionary simulations to shed light on the long-standing
 34 puzzle of animal play.

35 Keywords: play-fighting, social play, motor training hypothesis, evolutionary simulations,
 36 individual-based model, egalitarian–despotic

38 Introduction

39
 40 The functional significance of play behaviour in animals is an enduring puzzle in evolutionary
 41 biology (Graham & Burghardt 2010). Burghardt (2005) defined play as behaviour that is (i) not
 42 immediately necessary for current survival; (ii) spontaneous, done for its own sake; (iii) exaggerated,
 43 using modified patterns of other behaviours; (iv) repeated, but not in a manner that is rigidly
 44 stereotyped; and (v) performed in a stress-free environment. Note that none of these five criteria
 45 identifies a potential adaptive benefit. Evidence suggests that play involves short-term costs, such as
 46 increased exposure to predators (Blumstein, 1998), injuries (Berger, 1980) and energy costs to the
 47 players (Caro, 1995). Set against these costs, a range of hypotheses have been put forward to explain
 48 the evolution of play in terms of delayed benefits in adulthood — most prominently, that play is an
 49 aid to the development of adult motor skills (the ‘motor training’ hypothesis; Brownlee, 1954; Byers
 50 & Walker, 1995; Fagen, 1981). Observational studies have found some support for this hypothesis
 51 (Baldwin & Baldwin, 1976; Berghänel, Schülke, & Ostner, 2015; Byers & Walker, 1995; Lumia,
 52 1972). For example, Berghänel et al. (2015) found a positive correlation between juvenile locomotor

53 play and motor skills acquisition in Assamese macaques (*Macaca assamensis*), but also sizeable costs
54 of play in terms of reduction of growth. However, there are also conflicting results (e.g. Mancini &
55 Palagi, 2009; Sharpe, 2005) and no clear consensus on the adaptive significance of play has been
56 reached (Caro, 1988; Pellis & Iwaniuk, 1999).

57 Among the diverse forms of play, social play and, specifically, play-fighting are widespread
58 among juvenile mammals (Palagi et al., 2015; Pellis, Field, Smith, & Pellis, 1997; Pellis & Pellis,
59 2017). Play-fighting involves non-aggressive interactions in which one or more individuals gains
60 advantages over its counterparts (Aldis, 1975). Evidence suggests that play-fighting typically
61 includes elements of both competition (Symons, 1978) and cooperation (Altmann, 1962). The main
62 differences between cooperative and competitive aspects of play-fighting are summarised in Table 1,
63 following the competition/cooperation model (Reinhart, 2008; Pellis, Pellis, & Reinhart, 2010). The
64 dyadic nature of play-fighting is manifested differently in species with diverse societal organisation
65 and it has been suggested that competitive interactions are a particularly important aspect of
66 development in mammals that have a strong dominance hierarchy in adulthood (Chase, Tovey,
67 Spangler-Martin, & Manfredonia, 2002). If, as proposed by the motor-training hypothesis and several
68 other evolutionary explanations, play offers delayed benefits in adulthood (Graham & Burghardt,
69 2010), we might expect juvenile investment in play-fighting to covary across species with features of
70 the adult social environment, such as the societal structure and the level of adult aggression. In line
71 with this, numerous studies in the genus *Macaca* have shown a strong correlation across species
72 between the adult social environment and various features of juvenile social play, including the
73 duration of play sequences, the expression of different interaction patterns (e.g. wrestling), the
74 number of players involved and the use of certain body postures (Petit, Bertrand, & Thierry, 2008).

75 However, to make clear evolutionary predictions about patterns of play-fighting, it is crucial
76 to take into account the strong coevolutionary feedbacks that are likely to operate between juvenile
77 and adult social adaptations (Thierry, 2004). While play may promote the development of skills to
78 increase expected lifetime fitness, the magnitude of such benefits is likely to be strongly contingent

79 on environmental (including social) conditions and the decisions made in adulthood (e.g. aggressive
80 behaviour when competing for resources). This interplay can be challenging to study empirically, but
81 theoretical studies can provide important insights (Pellis, Burghardt, Palagi, & Mangel, 2015) and are
82 a particularly powerful tool when interactions between individuals affect population responses
83 (DeAngelis & Mooij, 2005). There have been only a few previous attempts to model play behaviour
84 in the literature (Durand & Schank, 2015; Grunloh & Mangel, 2015). For example, Durand and
85 Schank (2015) developed an evolutionary simulation based on the stag-hunt game (Rousseau, 1992)
86 to explore adult influences on juvenile social play, focusing on cooperation among individuals. Their
87 model predicted that play enhances social cohesion among juveniles and subsequently drives adult
88 cooperation.

89 In the present study, we develop a series of computer simulations in which juvenile strategies
90 for play-fighting can coevolve with adult strategies for competition over resources. Our focus is on
91 competitive forms of play-fighting that function to improve adult fighting skills, so our model should
92 be viewed as complementary to Durand and Schank's (2015) model of cooperative play-fighting. We
93 model a simple life cycle: individuals are born into a 'juvenile' stage in which they have play-fighting
94 interactions with other juveniles, before progressing (at a point determined by their evolved strategy)
95 to an 'adult' stage in which they have contests that determine their share of reproduction. We explore
96 the coevolutionary dynamics between juvenile play-fighting and adult competition under a range of
97 societal structures induced by variation in the degree of reproductive skew. If reproduction is
98 monopolised by a small number of individuals, competition between adults is expected to be fierce,
99 with disputes resolved using intense physical aggression, whereas societies in which all individuals
100 have a similar chance of reproducing are likely to be more peaceful (Hemelrijk, 2002). By inducing
101 such variation in the adult social environment and modelling its coevolution with juvenile play-
102 fighting, we can generate testable predictions about how patterns of juvenile play-fighting and the
103 intensity of adult competition should covary across species.

104 Following the motor training hypothesis, we assume that play may be costly in the short term
105 but that it enhances the development of motor skills that increase fitness pay-offs in adulthood
106 (Brownlee, 1954; Byers & Walker, 1995; Fagen, 1981). Specifically, investment in play-fighting is
107 assumed to increase an individual's strength and thereby improve its ability to win adult contests over
108 resources that determine the share of reproduction. Thus, investment in play-fighting confers a
109 delayed benefit in adulthood and should be most valuable when survival is high and successful adults
110 can expect a long reproductive career. Based on this assumed motor training benefit of play-fighting,
111 our initial expectations were as follows:

- 112 1. High investment in juvenile play-fighting should promote high levels of aggression in adult
113 contests; conversely, high levels of adult aggression should promote high juvenile investment
114 in play-fighting (to build up the necessary skills).
- 115 2. As the cost of injuries from losing adult fights increases, individuals should invest more in
116 play-fighting as a juvenile to improve their success in adult encounters, up to a point at which
117 the cost of injuries is so high that adult fighting is no longer favoured (in which case sharing
118 resources without aggression is preferred).
- 119 3. As background mortality rises, individuals should invest less in play-fighting and mature
120 sooner, because their expected lifespan is shorter and the value of their life is lower. They
121 should also become more willing to take risks and hence show a high level of aggression in
122 adult contests over access to reproduction.
- 123 4. Strong reproductive skew should lead to a 'fierce' society in which adults show intense
124 physical aggression to increase their chances of reproducing and juveniles invest in play-
125 fighting to improve their success in adult contests. Weak reproductive skew, by contrast,
126 should lead to a more 'peaceful' society in which both adult aggression and competitive
127 juvenile play-fighting are reduced, because reproduction is less dependent on the outcome of
128 adult contests.

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Methods

We modelled a population of $N = 1,000$ haploid individuals with two consecutive life stages: a juvenile stage in which they engage in play-fighting interactions with other juveniles, followed by an adult stage in which they compete with other adults for access to resources. Each individual has three evolvable genetic traits: m , x and y . The value of m specifies the number of play-fights the individual will engage in as a juvenile before maturing to adulthood ($m = 0,1,2,\dots$). The values of x and y ($x, y \in \mathfrak{R}$) determine its adult contest strategy as a function of its current strength s (see ‘Adult contests’, below). We track the evolution of these traits over a long sequence of discrete time steps, during which the following events occur: juvenile play-fights and adult contests; death from injury and background mortality; production of offspring to replace dead individuals; maturation of some individuals from the juvenile to the adult stage. We describe these events in turn below.

Juvenile play-fights

In each time step, juveniles are randomly assorted into dyads and engage in a play-fight, in which there is no winner or loser and no resources are at stake; if there is an odd number of juveniles, one of them (selected at random) does not interact in that time step. To represent the proposed motor training function of play-fighting (Brownlee, 1954; Byers & Walker, 1995; Fagen, 1981), we assume that the strength s of both participants increases by 1 unit as a result of the interaction. We also assume that there are no additional fitness costs of play-fighting beyond the background mortality rate experienced in all time steps (see ‘Mortality’, below).

Adult contests

Adults are randomly assorted into dyads and engage in contests over resources of fixed value V ; if there is an odd number of adults, one of them (selected at random) does not interact in that time step. These adult contests are modelled as a Hawk–Dove game (Maynard Smith & Price, 1973): if both

156 contestants play Dove, they share the resource (pay-off $V/2$ for each contestant); if one plays Hawk
157 and the other plays Dove, the former claims the resource (pay-off V) while the latter gains nothing
158 (pay-off 0); and if both play Hawk, they fight over it. In the event of a fight, the outcome is determined
159 by the contestants' relative strengths: the probability P that individual i defeats opponent j is given
160 by the logistic function $P = (1 + \exp[-b(s_i - s_j)])^{-1}$, where s_i and s_j are their respective strengths and b
161 is a parameter scaling the fighting advantage to the stronger individual ($b = 0$ indicates no advantage).
162 The winner of a fight gains the resource (pay-off V) while the loser gains nothing (pay-off 0) and
163 suffers an injury that with some small probability c results in its death ($c > 0$; see 'Mortality', below).
164 As for juvenile play-fights, we assume that engaging in a fight (i.e. but not in Hawk–Dove or Dove–
165 Dove contests) increases the strength of both individuals by 1 unit, up to a maximum of $s_{\max} = 1/d$
166 where d is the background probability of mortality (see 'Mortality', below).

167 Adult contest decisions are assumed to depend on their own strength. The probability of
168 playing Hawk (i.e. attacking the opponent), H , is given by the logistic function $H = [1 + \exp(x - ys)]^{-1}$,
169 where x and y are evolvable genetic traits that control, respectively, the inflection point of the function
170 and its steepness with respect to the individual's current strength s . In any given contest, this
171 probability is converted to a binary outcome by drawing a random number r from a uniform
172 distribution on the interval $[0,1]$ and noting whether $r < H$ (in which case the individual plays Hawk)
173 or $r \geq H$ (in which case it plays Dove).

174

175 *Mortality*

176 With probability c , the loser of an adult fight (see above) dies from their injuries. In addition, there is
177 a background mortality risk such that each time step a randomly selected fraction d of the population
178 (both juveniles and adults) die from causes independent of their behaviour. In both cases these
179 individuals are removed from the population and play no further part in the simulation. Note that in
180 the absence of any fighting the expected lifespan is $1/d$, which we set as the upper limit on strength

181 s_{\max} .

182

183 *Offspring production*

184 New offspring are produced to replace those individuals that have died from injuries incurred during
185 fights or from background mortality, such that the population size is maintained at $N = 1,000$. For
186 simplicity we model reproduction as an asexual process, with offspring inheriting their genetic values
187 of m , x and y from a single parent. With corresponding probabilities μ_m , μ_x and μ_y these values are
188 altered by mutation, by an amount drawn randomly from a uniform distribution (either 1, 2 or 3 in
189 the case of m , or from the continuous distribution $[0.0,0.4]$ in the case of x and y). The new offspring
190 are born into the juvenile stage and begin life with zero strength and resources.

191 Each offspring's parent is selected randomly with a probability proportional to $(\Sigma_n V)^\varphi$, where
192 the $\Sigma_n V$ is the total amount of resources it has accrued across all of its n adult contests so far and φ is
193 a reproductive skew parameter that controls the extent to which reproduction is monopolised by those
194 individuals with the most resources ($\varphi \geq 0$). A value of $\varphi = 0$ therefore represents a situation where
195 all adults have equal chance of reproducing regardless of their accumulated resources, while
196 increasing values of φ represent increasingly strong degrees of skew. We use this parameter to induce
197 variation in the intensity of adult competition along a continuum between 'peaceful' societies (low φ ,
198 implying weak benefits of excluding others from resources) and 'fierce' societies (high φ , implying
199 strong benefits of excluding others from resources).

200

201 *Maturation*

202 Before the next round of interactions, the age (measured in number of time steps) of each surviving
203 individual is incremented by one unit. Any juveniles who have reached their maturation point (i.e.
204 their age is equal to m time steps) leave the juvenile stage and move to the adult stage, starting with
205 the value of s they had achieved through play-fighting.

206

207 This sequence of events repeats in each time step of the simulation. We initialised each simulation
208 with genetic values $m = 0$, $x = 0$ and $y = 0$ for all individuals, such that they mature immediately
209 (without any investment in play-fighting) and then choose Hawk and Dove with equal probability in
210 adult contests (regardless of their strength). We then tracked changes in juvenile play-fighting and
211 adult aggression across the time steps, as the genetic values of m , x and y coevolved in response to
212 selection. To represent the outcomes, we computed the following summary statistics: the relative
213 investment in play-fighting as a fraction of the expected lifespan, m/d , which is influenced by the
214 evolved value of m ; and the proportion of adult encounters that escalate into physical fights, p_{fight} ,
215 which is influenced by the evolved values of x and y . Table 2 lists the model parameters and their
216 default values (i.e. the values used when systematically varying other parameters). The model was
217 written in C++ and the code is provided as supplementary information (online appendix A).

218

219

Results

220

Trajectory of coevolution between adult aggression and juvenile play-fighting

222 We simulated the coevolution of m , x and y over 50,000 time periods, running 20 replicate simulations
223 for each parameter combination. In all simulations, both adult aggression and juvenile play-fighting
224 initially increased, but thereafter their coevolution led to one of two outcomes: a high-play, high-
225 aggression outcome in which the evolved values of both m/d and p_{fight} were close to 1, or a low-play,
226 low-aggression outcome in which they were both close to zero (note that low-play, high-aggression
227 and high-play, low-aggression outcomes were never seen). Which of the two outcomes resulted
228 depended on the values of c and d , as shown in Fig. 1. Lower injury costs of losing a fight ($c = 0.1$)
229 favoured escalated aggression in adult contests preceded by an extended period of juvenile play-
230 fighting (high-play, high-aggression; Fig. 1, top row), whereas high injury costs ($c = 0.4$) favoured
231 more passive resolution of adult contests and minimal investment in juvenile play-fighting (low-play,
232 low-aggression; Fig. 1, bottom row). For intermediate injury costs ($c = 0.2, 0.3$) the high-play, high-

233 aggression outcome was favoured only at high background probabilities of mortality d , associated
234 with a shorter expected lifespan (Fig. 1, middle rows). In some cases, the coevolutionary trajectory
235 occasionally fluctuated between the high-play, high-aggression and low-play, low-aggression
236 outcomes (e.g. for $c = 0.3$, $d = 0.1$; Fig. 1, right-hand panel, third row), indicating that intermediate
237 levels of juvenile play-fighting and adult aggression were not evolutionarily stable.

238

239 *Adult contest strategy*

240 Fig. 2 shows the evolved strategy for adult aggression (probability of playing Hawk, H) and the
241 evolved maturation point (m) under three of the parameter combinations shown in Fig. 1, with Figs
242 2A ($c = 0.1$, $d = 0.05$) and 2B ($c = 0.3$, $d = 0.1$) corresponding to high-play, high-aggression outcomes
243 and Fig. 2C ($c = 0.4$, $d = 0.05$) corresponding to a low-play, low-aggression outcome. In all three
244 cases the curves typically plateau before (or soon after) the maturation point, indicating that the
245 tendency to escalate adult conflicts is relatively insensitive to current strength. In the high-play, high-
246 aggression outcomes, juveniles build up their strength over a prolonged period of play-fighting and
247 then always attack their opponent when they reach adulthood (Fig. 2A,B). In the low-play, low-
248 aggression outcome, in contrast, they mature early in life with very limited play-fighting experience,
249 and then always play Dove as an adult (Fig. 2C).

250

251 *Impact of reproductive skew on coevolutionary outcomes*

252 The degree of reproductive skew (φ) has a pronounced impact on the coevolution between juvenile
253 play-fighting and adult aggression. Strong reproductive skew ($\varphi > 1$), representing greater
254 monopolisation of resources, favours high aggression in adulthood (Fig. 3A), i.e. a 'fierce' society,
255 and high investment in juvenile play-fighting (Fig. 3B). Weaker skew ($\varphi < 1$), representing more
256 equitable sharing of reproduction, leads to low levels of adult aggression (Fig. 3A), i.e. a more
257 'peaceful' society, and limited juvenile play-fighting (Fig. 3B). The switch between these two

258 outcomes is abrupt, again suggesting that intermediate levels of adult aggression and juvenile play-
259 fighting are not evolutionarily stable.

260

261

Discussion

262

263 Our simulations showed that coevolution between juvenile play-fighting and adult aggression
264 resulted in one of two outcomes. One outcome was a high-play, high-aggression situation in which
265 almost all adult contests escalate into physical fights and individuals spend a substantial part of their
266 lives preparing for this fierce competitive environment through an extended juvenile period of play-
267 fighting. The other outcome was a low-play, low-aggression situation in which almost all adult
268 contests are resolved peacefully by sharing the contested resources without any escalation, and there
269 is minimal investment in play-fighting early in life before juveniles progress to the adult stage. In
270 both cases, the evolved adult contest strategy is relatively insensitive to variation in strength, either
271 because by the time they mature individuals are always willing to escalate contests regardless of their
272 own strength (high-play, high-aggression outcome), or because they are seldom willing to do so (low-
273 play, low-aggression outcome). Intermediate levels of adult aggression combined with moderate
274 investment in play-fighting appear not to be evolutionarily stable. Which of the two outcomes results
275 depends on the probabilities of death from injuries sustained during fights (c) and from background
276 causes independent of behaviour (d), and on the strength of reproductive skew (ϕ). The high-play,
277 high-aggression outcome is favoured by low injury costs of losing fights (low c), low expected future
278 fitness prospects associated with a high background mortality rate (high d), and strong reproductive
279 skew (high ϕ). The low-play, low-aggression outcome is favoured by high injury costs (high c), high
280 expected future fitness (low d) and weak reproductive skew (low ϕ).

281

282 We first briefly discuss how the pattern of adult aggression in our simulations relates to the
283 predictions from game-theoretic models of animal conflict. In their model of repeated Hawk–Dove
contests in a population with no variation in strength, Houston and McNamara (1991) showed that a

284 pure Hawk strategy ($H = 1$) is favoured when deaths from injury are rare (low c) but background
285 mortality (d) is high. These conditions also favoured the high-aggression outcome in our simulations
286 (Fig. 1), where strength could vary among individuals (due to differences in age and previous (play-
287)fighting experience) and individuals randomly encountered both weaker and stronger opponents.
288 Models by Crowley (2000) and McNamara and Houston (2005) incorporated variation in strength in
289 a standard (non-repeated) Hawk–Dove game and predicted that when an animal knows its own
290 strength but not that of its opponent (as assumed in our simulations) the evolutionarily stable strategy
291 (ESS) is to play Hawk above a threshold level of strength and Dove otherwise. McNamara and
292 Houston showed that this could lead to a stable intermediate level of fighting, providing losing fights
293 is not too costly relative to the value of winning. In our simulations the evolved contest strategy does
294 fit the predicted form, with a sudden switch from one behaviour to another above a threshold level of
295 strength (Fig. 2), but unlike McNamara and Houston we found only very high ($p_{\text{fight}} \approx 1$) or very low
296 ($p_{\text{fight}} \approx 0$) levels of fighting (Figs 1,3). A key difference is that whereas McNamara and Houston
297 assumed that variation in strength was fixed, in our simulations individuals could increase their
298 strength through play-fighting and adult fighting. For conditions conducive to aggressive behaviour
299 (low c and high d), all individuals tended to escalate adult contests because their juvenile investment
300 in play-fighting ensured that their strength at maturation was above the threshold for playing Hawk.
301 This explains why intermediate levels of fighting were not stable in our simulations.

302 Below we discuss the theoretical predictions of our model, the extent to which they are
303 empirically supported and some possible directions for future work.

304

305 *Relationship between adult aggression and juvenile play-fighting*

306 Across simulations, adult aggression and juvenile play-fighting were positively correlated: high levels
307 of adult aggression select for greater investment in play-fighting in the juvenile phase, and,
308 reciprocally, high levels of play-fighting increase the expected pay-off from behaving aggressively
309 as an adult. This was expected (Hypothesis 1), given that the motor training mechanism we

310 implemented in the model enables individuals to increase their adult fighting ability through engaging
311 in play-fighting as juveniles. Although this is a commonly assumed function of play (Byers and
312 Walker 1995; Potegal and Einon 1989; Taylor 1980), to our knowledge it has not been established
313 whether rates of juvenile play-fighting are correlated with the intensity of adult aggression across
314 species; testing this prediction using phylogenetically controlled analyses would be a useful direction
315 for future research.

316 Within species, there is mixed evidence that rates of play and adult aggression are linked. Play
317 is positively correlated with later fighting skills in rats (*Rattus rattus*) and those individuals that play-
318 fight most are more aggressive overall (Taylor, 1980). In Syrian golden hamsters (*Mesocricetus*
319 *auratus*), Pellis and Pellis (1988) found that increased levels of play-fighting were linked to greater
320 values of later aggression. However, in a long-term study of meerkats (*Suricata suricatta*), Sharpe
321 (2005) found no association between the frequency of play-fighting and adult fighting success. Some
322 studies support a more general role of play in the development of adult skills. In Belding's ground
323 squirrels (*Spermophilus beldingi*), high rates of juvenile social play are associated with greater motor
324 skills in adulthood, potentially leading to advantages in resource acquisition for squirrels that played
325 more as juveniles (Nunes et al., 2004). Positive correlations between playfulness and skilfulness have
326 also been found in common marmosets (*Callithrix jacchus jacchus*), in which wrestling behaviour
327 facilitates avoidance of obstacles (Chalmers & Locke-Haydon, 1984), and in some species enhanced
328 adult skills through play may reflect greater development of social cognition and associated neural
329 circuits (Lewis, 2000; Pellis, Pellis, & Himmler, 2014).

330 Our model assumes that juvenile play-fighting is a form of practice for adult fighting, but
331 there is evidence that play-fighting has broader relevance for adult behaviour. Deprivation
332 experiments, in which the opportunity for individuals to engage in play-fighting is artificially
333 restricted, reveal a wide range of social and emotional deficits rather than a specific effect on fighting
334 ability, suggesting that play is important more generally in the development of social competence
335 (Pellis et al., 2014). For example, studies on rats and hamsters have shown that limiting juvenile play

336 experiences leads to impaired social skills and emotional regulation, accompanied by
337 neuroanatomical changes in the prefrontal cortex (Bell et al., 2010; Burleson et al., 2016; Schneider
338 et al., 2016; van den Berg et al., 1999). Models focused on more cooperative elements of play
339 behaviour, such as that by Durand and Schank (2015), may be needed to explain some of these
340 impacts on adult social relationships.

341

342 *Effects of mortality risk in fights and from other sources*

343 Whether coevolution led to the high-play, high-aggression outcome or the low-play, low-aggression
344 outcome was strongly affected by the mortality risks, both from injuries sustained during fights and
345 from background sources independent of behaviour. When losing fights is costly (high c), selection
346 favours reduced adult aggression and more amicable sharing of resources (in support of Hypothesis
347 2), which in turn lowers the incentive to engage in play-fighting. There is some empirical support for
348 a negative relationship between injury risk and adult aggression: in roe deer (*Capreolus capreolus*),
349 asymmetry in antler size increases the probability of dying in an encounter and decreases the number
350 of escalated contests (Hoem, Melis, Linnell, & Andersen, 2007). We also observed that, while c was
351 still low enough to favour the high-play, high-aggression outcome, there was a slight increase in play
352 investment with increasing c (e.g. for $d = 0.1$ [right-hand column] in Fig. 1, compare $c = 0.1$ [top row]
353 with $c = 0.2$ [second row]). This is because when adult contests are more risky (high p_{fight} combined
354 with moderately high c), it becomes particularly important to increase fighting ability through
355 juvenile play-fighting.

356 Increasing the background mortality rate (d) shortens the expected lifespan, which reduces the
357 expected fitness from future encounters and favours a more short-term perspective (a form of the
358 asset-protection principle; Clark, 1994). In our simulations, this selected for more risky, aggressive
359 behaviour in adult contests, in line with Hypothesis 3. However, contrary to our expectations, higher
360 background mortality did not select for reduced investment in play-fighting (as a proportion of the
361 expected lifespan): rather, because of the coevolutionary feedback between adult and juvenile

362 strategies, high values of d favour a relatively extended period of juvenile play-fighting (within the
363 constraints of a shortened lifespan) to prepare for the more aggressive adult environment. This is an
364 interesting prediction because it contradicts previous suggestions, based on energetic costs, that the
365 frequency of play behaviour should decline under harsh environmental conditions (Martin, 1982), for
366 which there is some empirical support within species (Barrett, Dunbar, & Dunbar, 1992; Lee, 1984).
367 This hypothesis ignores the possibility that those same conditions are also likely to influence adult
368 competition over resources, which as our simulations highlight can have a strong impact on selection
369 for play. For a clearer understanding of the conditions under which play behaviour is favoured, we
370 urge researchers to consider the adult social environment alongside variation in resource availability
371 and other extrinsic factors.

372

373 *Effect of reproductive skew*

374 Whether coevolution led to the high-play, high-aggression outcome or the low-play, low-aggression
375 outcome was also strongly affected by the degree of reproductive skew (ϕ), in terms of the extent to
376 which reproduction was monopolised by those with the most resources. As expected (Hypothesis 4),
377 strong reproductive skew ($\phi > 1$) favours high aggression in adulthood preceded by an extended
378 period of juvenile play-fighting, whereas weaker skew ($\phi < 1$) favours amicable sharing of resources
379 and only a brief period of play-fighting before progressing to the adult stage. Thus our model predicts
380 that, all else being equal, animals that live in ‘fierce’ societies should invest more in juvenile play-
381 fighting than those that live in relatively peaceful societies.

382

383 *Empirical evidence in Macaca*

384 We examined empirical support for the predicted pattern of co-variation between adult societal
385 structure and juvenile play-fighting using data from the genus *Macaca*, where there is substantial
386 variation in dominance styles. Thierry (2000) classified the 18 species in this genus according to their
387 social system, along a continuum from so-called ‘despotic’ to ‘egalitarian’ systems. The most

388 despotic systems (grade 1), seen in *M. mulatta*, *M. fuscata* and *M. cyclopis*, are characterised by
389 unequal distribution of reproductive opportunities between dominants and subordinates, kin-centric
390 power asymmetries and higher incidence of biting by dominants in within-troop disputes (Aureli,
391 Das, & Veenema, 1997; Caldecott, 1986; Kutsukake & Castles, 2001; Thierry, 1985). In the most
392 egalitarian systems (grade 4), by contrast, seen in *M. tonkeana*, *M. maura*, *M. nigra*, *M. nigrescens*,
393 *M. hecki* and *M. ochreata*, access to resources is less constrained by kinship ties, interactions are less
394 aggressive and biting less frequent but more likely to be reciprocated (Butovskaya & Kozintsev
395 1996). Applying the predictions of our model we might therefore expect that despotic species would
396 show greater investment than egalitarian species in juvenile play-fighting, as preparation for a more
397 fiercely competitive adult environment.

398 In the few studies directly comparing the play behaviour of a despotic species (*M. fuscata*)
399 with an egalitarian species (either *M. tonkeana* or *M. nigra*), no difference was reported in the overall
400 frequency of play (Petit et al. 2008, Reinhart et al. 2010; Scopa & Palagi 2016). Across other studies,
401 methodological differences, the use of both captive and free-living groups, variation in housing
402 conditions and the lack of consistent or standardised measures makes it difficult to compare the
403 overall frequency of play-fighting across species. However, for seven of the 18 species classified by
404 Thierry (2000) there are some data on the extent to which play-fighting is competitive or cooperative
405 (Petit et al., 2008; Reinhart, 2008; Reinhart et al., 2010). Table 3 summarises variation in the style of
406 play-fighting across these seven species, ranging from the despotic *M. mulatta* and *M. fuscata* to the
407 egalitarian *M. tonkeana* and *M. nigra*. The general pattern is that egalitarian species, such as Tonkean
408 macaques (*M. tonkeana*) and crested macaques (*M. nigra*), adopt a more cooperative style of social
409 play than the competitive play-fighting seen in despotic species such as Japanese macaques (*M.*
410 *fuscata*), with egalitarian species showing more reciprocal rough-and-tumble play (e.g. higher
411 frequency of wrestling) and despotic species more cautious play (e.g. face-to-face body orientation
412 between partners to avoid vulnerable positions; Ciani, Dall'Olio, Stanyon, & Palagi, 2012; Palagi et
413 al., 2015; Petit et al., 2008; Reinhart, 2008; Reinhart et al., 2010; Scopa & Palagi, 2016; Thierry,

414 1985, 2000). For example, Tonkean macaques engage in longer bouts of play and have a relatively
415 cooperative style of play-fighting compared to the more competitive style of play-fighting in Japanese
416 macaques, which involves different behavioural patterns and preferred body targets (Ciani et al.,
417 2012; Reinhart et al., 2010).

418

419 *Limitations and future directions*

420 The pattern across macaque species provides only partial support for our model. The greater emphasis
421 on competitive elements of play-fighting in more despotic species fits with the idea that this serves
422 as practice for potentially dangerous adult fighting. At the same time, our model is unable to account
423 for investment in other, more cooperative elements of play seen in more egalitarian species. The
424 motor training mechanism we implemented may not be appropriate for egalitarian societies, in which
425 play may instead have evolved to promote social cohesion (Ciani et al., 2012; Palagi 2006). It has
426 been suggested that more egalitarian species show more adult–adult play, which enhances social
427 cohesion across individuals, whereas more despotic species prioritise adult–juvenile play, which has
428 a teaching function for the young (social bridge mechanism; Mancini & Palagi, 2009). This limits the
429 scope of our model and highlights that, rather than being a unitary phenomenon, different forms of
430 play-fighting may require different functional explanations. In this regard, the combination of our
431 own model (focused on competitive play-fighting) and Durand and Schank’s (2015) model (focused
432 on cooperative play-fighting) may together offer a more satisfactory explanation for patterns of play-
433 fighting than either model alone. However, it is difficult to draw firm conclusions because the data
434 are so patchy. A useful direction for future work would be to collect more systematic, directly
435 comparable data on the relative investment in competitive versus cooperative play-fighting across the
436 *Macaca* genus, to establish more clearly how this relates to the despotic–egalitarian spectrum of
437 dominance hierarchies.

438 Besides incorporating other proposed functions of play-fighting, our model could be extended
439 in a number of useful directions. The present implementation had no explicit representation of males

440 and females, instead (for simplicity) modelling reproduction as asexual and considering all
441 individuals to be of the same type. Modelling separate dominance hierarchies for males and females
442 would potentially allow us to predict sex differences in the intensity of adult aggression and patterns
443 of play-fighting behaviour. Another possibility would be to incorporate sexual dimorphism and
444 intrasexual variation in weaponry (e.g. canine size), to investigate how this affects the willingness to
445 escalate disputes into physical fights. It would also be interesting to study how pre-existing
446 differences in fighting ability, which may subsequently be amplified or dampened by motor training,
447 would affect the predicted patterns of juvenile play-fighting and adult aggression. We leave these
448 possible extensions to future work.

449

450 *Conclusion*

451 Despite decades of research and a wealth of empirical data, the adaptive significance of play-fighting
452 behaviour remains unclear. The model we have presented here, implementing the motor training
453 hypothesis, adds to a small number of theoretical studies on play-fighting, which are invaluable in
454 refining predictions and identifying the conditions under which play-fighting is expected to evolve.
455 Our model highlights the importance of considering play-fighting behaviour in a broader life-history
456 context, taking into account its coevolution with the adult social environment—in particular, the
457 intensity and aggressiveness of adult competition. A comparison of empirical findings from despotic
458 and egalitarian macaque societies reveals the need for more directly comparable data and also
459 underscores the limited scope of our model, suggesting that play-fighting is more likely a
460 multidimensional phenomenon with different adaptive functions applying to competitive and
461 cooperative forms of play. More empirical and theoretical studies are needed to investigate how and
462 why play-fighting has evolved, what consequences this has for shaping adult aggression and
463 conversely how adult competition under different societal structures affects juvenile investment in
464 play-fighting.

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Tables

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Table 1

Comparison between cooperative and competitive aspects of play-fighting, based on Reinhart (2008) and Pellis, Pellis and Reinhart (2010)

Cooperative play	Competitive play
Attacks are concentrated on species-typical playful body targets, rather than agonistic ones	Agonistic body targets are more often involved
Lack of defensive elements in play sequences	Defensive component is present
Play body targets are exposed to the partner	Body targets are protected or hidden from the partner
Frequent role reversals of attacker and defender occur during a single play bout with the same partner	Role reversals are prevented or resisted
Play-fighting occurs with many different peers, sometimes with multiple individuals at the same time (i.e. polyadic play)	Play-fighting interactions are brief and only a few different partners are involved

630

631

Table 2

Parameters of the model and their default values

Symbol	Interpretation	Default value
V	Value of resources at stake in each adult contest	1
b	Fighting advantage to a stronger individual	0.5
c	Probability of death from injuries when losing a fight	0.3
d	Background probability of mortality per time step	0.1
φ	Reproductive skew parameter, determining how strongly reproduction is monopolised by those with most resources	1.0
N	Population size	1,000
μ_m	Probability of mutation in value of genetic trait m	0.05
μ_x	Probability of mutation in value of genetic trait x	0.05
μ_y	Probability of mutation in value of genetic trait y	0.05

632

633

634

Table 3

Description of social system (from 1 = despotic to 4 = egalitarian) and the style of play-fighting in seven *Macaca* spp.

Species	Social system ^{†1}	Style of play-fighting
<i>M. mulatta</i>	1	mixed ^{‡2,3,4,5,6}
<i>M. fuscata</i>	1	mainly competitive ^{2,7,8,9}
<i>M. fascicularis</i>	2	mainly competitive ^{‡2}
<i>M. sylvanus</i>	3	mainly competitive ^{‡2,10}
<i>M. radiata</i>	3	mixed ²
<i>M. tonkeana</i>	4	mainly cooperative ^{8,9}
<i>M. nigra</i>	4	mainly cooperative ^{7,11}

635 † The social system is characterised along the despotic–egalitarian continuum. Grade 1 = most despotic;
 636 unequal distribution of reproductive opportunities between dominants and subordinates and kin-centric power
 637 asymmetry (Aureli, Das & Veenema, 1997; Katsukake & Castles 2001). Grade 4 = most egalitarian; less
 638 constrained by kinship ties in accessing resources and characterised by more friendly interactions (Butovskaya
 639 & Kozintsev 1996).

640 ‡ Classification of play-fighting style in *M. mulatta*, *M. fascicularis* and *M. sylvanus* is tentative, based on
 641 available descriptions in the literature (Symons, 1978; Levy, 1979; Tartabini & Dienske, 1979; Caine &
 642 Mitchell, 1979; Pellis et al., 2010); more systematic data are needed to confirm the nature of play-fighting in
 643 these species.

644 References: ¹Thierry, 2000; ²Caine & Mitchell, 1979; ³Pellis et al., 2010; ⁴Levy, 1979; ⁵Tartabini & Dienske,
 645 1979; ⁶Symons, 1978; ⁷Petit et al., 2008; ⁸Reinhart et al., 2010; ⁹Scopa & Palagi, 2016; ¹⁰Kipper & Todt,
 646 2002; ¹¹Nickelson & Lockard, 1978.

647

648

Figure legends

649

650 **Figure 1.** Coevolutionary trajectories (over 50,000 time steps) of adult aggression (proportion of
 651 contests that escalate into a fight, p_{fight}) and relative investment in juvenile play-fighting as a fraction
 652 of expected lifespan (m/d ; population mean values), for varying probabilities of death from
 653 background sources ($d = 0.05, 0.075, 0.1$, increasing left to right) and from injuries sustained during
 654 fighting ($c = 0.1, 0.2, 0.3, 0.4$, increasing top to bottom). Grey lines show the values from 20 replicate
 655 simulation runs, while the black line shows the median across all replicates, with points plotted every
 656 100 time steps. The grey square indicates the starting point of the simulations ($p_{\text{fight}} = 0$ and $m/d = 0$,
 657 at time step 0) and the numbers next to the grey circles indicate how many thousands of time steps
 658 have elapsed by that point. Other parameter values: $V = 1$, $b = 0.5$, $\varphi = 1.0$, $N = 1,000$, $\mu_m = \mu_x = \mu_y =$
 659 0.05 .

660

661 **Figure 2.** Adult contest strategy (probability of playing Hawk, H) as a function of strength (s) based
 662 on evolved population mean values of x and y after 50,000 time steps, for the following probabilities
 663 of death from background sources (d) and from injuries sustained during fighting (c): **(A)** $c = 0.1$, d
 664 $= 0.05$; **(B)** $c = 0.3$, $d = 0.1$; **(C)** $c = 0.4$, $d = 0.05$. The vertical arrows indicate the evolved population
 665 mean values of the maturation point m (number of time steps spent play-fighting as a juvenile, before
 666 transitioning to the adult stage). Grey curves and arrows show the values from 20 replicate simulation
 667 runs, while the black curve and arrow show the median across all replicates. Other parameter values:
 668 $V = 1$, $b = 0.5$, $\varphi = 1.0$, $N = 1,000$, $\mu_m = \mu_x = \mu_y = 0.05$.

669

670 **Figure 3.** Evolved levels (after 50,000 time steps) of **(A)** adult aggression (proportion of contests that
 671 escalate into a fight, p_{fight}) and **(B)** investment in juvenile play-fighting (number of time steps before
 672 maturing, m ; population mean values), for varying degrees of reproductive skew (parameter φ). Black
 673 dots show the values from 20 replicate simulation runs, while the grey boxes show the median and

674 interquartile range (IQR) across all replicates (with whiskers extending to $1.5 \times \text{IQR}$). Other
675 parameter values: $V = 1$, $b = 0.5$, $c = 0.3$, $d = 0.1$, $N = 1,000$, $\mu_m = \mu_x = \mu_y = 0.05$.

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