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Juvenile survival and benefits of play behaviour in brown bears, *Ursus arctos*

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ABSTRACT

The play of healthy, well-fed young mammals and birds includes varied and improvised behavioural routines and occurs in relatively stress-free contexts. Play behaviour has evolutionary costs but no apparent benefits. Play, therefore, poses a problem for evolutionary theory. Theory on play generally assumes future (adult) benefits, but benefits of animal play may be short term. In a 10-year field study, we measured play and survival in young of 11 families of individually identified, free-ranging brown bears, *Ursus arctos*. Our results are the first to relate play to survival. Cubs who played more during their first summer survived better from their first summer to the end of their second summer. To explain this apparent association, we applied statistical controls to three potential confounding factors: cub condition, prenatal and first-year salmon availability, and maternal characteristics. Controlling for these factors, we confirmed that survival increases as play increases, independently of these other possible effects. Play can have demonstrable and measurable evolutionary and population consequences if it increases short-term survival of immatures. Mechanisms linking play of bears or of other animals to short-term survival are not yet known. We speculate that play experience relieves past stress and builds resistance to future stress. We cite known neuroendocrinological mechanisms that may support this suggestion.

Keywords: Alaska, brown bear, play behaviour, survival, *Ursus arctos*.

INTRODUCTION

Play characterizes the behaviour of young mammals and birds (Fagen, 1981; Power, 2000). Frequent and complex play occurs in taxonomic orders whose members have large brains relative to body size (Iwaniuk *et al.*, 2001). Energy costs of play ultimately reduce future reproductive success (e.g. Sharpe *et al.*, 2002). Costly behaviour like play must have benefits (Sharpe *et al.*, 2002) or else involve fundamental constraints. Benefits of animal play, and therefore its evolutionary significance, remain unclear (Caro, 1988; Pellis and Iwaniuk, 1999). Long viewed as preparation for adulthood, play of immatures may in theory be

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most important over shorter developmental time-scales (Martin and Caro, 1985; Caro, 1995). Biben and Champoux (1999) showed that play and cortisol, a measure of stress, covaried negatively in young *Saimiri*. Their results suggested short-term advantages for play experience. Here we examine possible associations between play and short-term survival in young brown bears.

Individual condition, food availability and maternal characteristics all influence short-term survival of immatures (Clutton-Brock, 1991; Wachter and Bulatao, 2003). We address play and survival in the context of these factors.

In this paper, the term 'litter' denotes a set of cubs first seen at the beginning of the field season in July of their natal year. 'Survival' and 'first-year survival' denote survival from the beginning of the field season in early July of their natal year to the end of the field season in late August of their second year.

METHODS

We observed individually identified, free-ranging brown bears, *Ursus arctos*, at Pack Creek, Admiralty Island, southeastern Alaska in July to August, 1985–1994 (Fagen and Fagen, 1996). In each of these 10 successive annual field seasons, observers spent at least 600 h on site, using focal-animal sampling methods to estimate percent time each individual spent playing.

Brown bear play includes wrestling, chasing, locomotion and body rotation, and object manipulation, accompanied by characteristic facial expressions and body movements (Fagen, 1981). We used several criteria for play:

- Play is silent, but loud vocalizations accompany aggressive displays and escalated fights.
- Playing bears have a specific facial expression, the relaxed open-mouth grin or play-face.
- In play, a bear characteristically twists its torso in a plane perpendicular to the long axis of the body by dropping one shoulder while simultaneously lifting the other shoulder and the front leg and paw on the same side as the lifted shoulder. Anatomically, this movement consists of a transverse planar rotation of the upper torso initiated in the upper back and resulting in adduction of the foreleg on one side of the body.

We identified 14 families with 1–3 cubs. No family had more than 3 cubs. Eleven of these families (19 cubs) used the study site regularly and were each observed for 13 h or more during their first summer. All mothers returned the following summer and were again observed for at least 13 h.

We observed no actual mortality. When cubs did not return with their mothers and were not observed during the year following their birth, we assumed they did not survive. The percentage of each litter of cubs-of-the-year (spring cubs) surviving from the first week of July of their natal year to the third week of August of the following year was termed first-year survival.

When salmon are abundant, coastal brown bear females produce more surviving offspring (Hilderbrand *et al.*, 1999; Ferguson and McLoughlin, 2000). To measure salmon availability, we used the weighted sum of pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon abundance based on annual State of Alaska estimates for Pack Creek. We defined salmon availability = (pink numbers + 3 times chum numbers) to reflect species differences in average weight. In this paper, 'fish' will denote this measure of overall salmon availability.

Ratings

We assessed cub condition by rating (Hinde, 1979; Feaver *et al.*, 1986; Fagen *et al.*, 1997) each of the 11 litters on a scale of 1–5. We averaged our results to yield an overall condition score for each litter (Kendall's tau for observers' independent ratings = 0.4, $P = 0.03$). To verify our ratings of cub activity, we correlated these ratings with a direct behavioural measure of cub activity. We defined this behavioural measure as the difference between percent time in sight spent in active behaviour and percent time in sight spent in sedentary behaviour. Travelling and fishing constitute active behaviour. Resting by a cub is sedentary behaviour, as is waiting while the cub's mother is fishing.

We rated each of the 8 mothers on 21 personality characteristics found to be reliable ($r \geq 0.70$) in a previous study of individual distinctiveness in brown bears (Fagen and Fagen, 1996). Some of these characteristics (e.g. careless, insecure, irritable) addressed maternal behaviour directly. Others (e.g. expert at fishing, hostile to other bears) involved aspects of the environment relevant to offspring well-being and survival. Mean ratings of the two observers on each of these 21 reliable characteristics (see Appendix 1; definitions in Fagen and Fagen, 1996) were analysed to define characteristics of maternal behaviour (see Data analysis).

Data analysis

The unit of analysis for this study was the litter. We defined survival as the fraction of cubs in a litter surviving from the beginning of the field season in their natal year to the end of the field season in the following year.

We used linear statistical models (Chambers, 1992; Neter *et al.*, 1996) to examine survival in relationship to condition, to salmon availability and to play. The models included play (percent time in sight spent playing, averaged over all cubs in a litter), condition rating and the sum of prenatal and natal year salmon availability as continuous variables. We transformed summed salmon availability (square root transformation) to obtain better numerical properties. In all likelihood, zero values for condition, salmon availability and play would produce zero survival. Therefore, models of survival as a function of these variables would necessarily pass through the origin. For this reason, fitted models estimate no intercept.

We used product–moment (Pearson) partial correlation coefficients (Neter *et al.*, 1996) to measure relationships between survival and play in the presence of other variables. We used exact permutation tests (Edgington, 1995) to assess the statistical significance of these partial correlation coefficients. Specifically, given values of adjusted survival and adjusted play for our sample of 11 litters, we computed the correlation coefficient of adjusted survival and adjusted play for each possible permutation of the adjusted survival values. The (one-sided) P-value for the permutation test is the number of partial correlations obtained from the permuted data that exceed or are equal to the partial correlation obtained from the actual (unpermuted) data. We used one-sided permutation tests to assess the statistical significance of play in relation to survival because a negative correlation of play with survival would be equivalent to failure to reject the null hypothesis of no enhancement of survival by play.

We used a three-predictor linear model ('full' model) of survival with condition, salmon availabilities and play as variables. To assess the fit of the model to the data, we tested the multiple correlation coefficient by calculating its value for each distinguishable permutation of the survival values with the same predictor values, then comparing the resulting correlations with the actual value using a two-sided permutation test. (Equivalently, permutation tests of the overall *F*-statistic for the model yielded the same results.) To determine possible simplifications to the full model, we used C_p graphs and backward stepwise model selection methods (Chambers, 1992; Neter *et al.*, 1996).

We used Chambers' (1992) method to analyse sensitivity of linear models to possible uncertainties in their predictor variables. We first chose plausible values for the uncertainty in each predictor value. Next, we divided the predictor values by these uncertainty values to define scaled predictor values. Using these scaled predictor values (Chambers, 1992), we then computed singular-value decompositions (Golub and van Loan, 1989) of the predictor matrices.

We used Cook's distance (Neter *et al.*, 1996) to measure the numerical influence of single data points on each model fit to the data. Any data point having a Cook's distance ≥ 1 merits additional scrutiny. And any data point having a Cook's distance ≥ 4 will almost surely produce misleading results when the model is fit (Glantz and Slinker, 2001).

Components of variation among mothers, as measured by our ratings of mothers' individual characteristics, might affect survival. Such effects could confound attempts to detect effects of play *per se* on first-year survival. For this reason, we used two different approaches to the ratings: a grouping method (Feaver *et al.*, 1986; Fagen and Fagen, 1996) and principal components analysis. These analyses sought to extract different general factors from our ratings of mothers' personalities. These general factors might capture maternal effects in a way that coding maternal identity could not. Contrasting mothers in this manner yields a parsimonious, reduced-dimensional approach to possible maternal effects. We calculated the partial correlation of survival (adjusted for cub condition and salmon availability) with each variable extracted and tested each correlation by randomization. We sought aspects of individual distinctiveness among mothers that might produce variation in survival even among cubs in the same condition.

To verify that our results did not depend on the choice of a particular linear modelling approach, we also analysed the data using generalized linear models with logit link and binomial variance ('logistic regression'). To make the logistic regression models more nearly comparable to the regression models with no fitted intercept, we assumed a value of -18.4 for the constant term in the linear predictor, corresponding to a survival probability of 10^{-8} when condition, fish and play are all zero.

The grouping method for identifying separate dimensions of personality variation (Feaver *et al.*, 1986) defines sets of associated traits based on correlations of mean ratings. Fagen and Fagen (1996) applied this method to brown bears. Principal components analyses used the eight mothers as sampling units and the 21 personality characteristics as variables.

We used the S-Plus 6 for Windows data analysis system (Insightful Corp., Seattle, WA). We used default values for all analyses except for those involving generalized linear models, where we used a maximum of 5000 iterations and a tolerance of 0.00001 (Venables and Ripley, 1999).

RESULTS

No cubs from 7 of the 11 families returned. All six cubs from 3 of the original 11 families and two cubs from a fourth family survived from the beginning of their second summer to the beginning of their third summer. All but one of these surviving eight cubs survived to independence at the beginning of their third or fourth summer.

Of the 19 cubs we observed, only one died during its first summer. All other apparent mortality occurred sometime between late August of the cubs' first year and early July of their second year. Seven of eight multiple-cub litters either survived or did not survive as a whole: one litter of three cubs had two survivors, and all other litters survived or did not survive as a whole to the end of their second summer. Consequently, three litters had a survival fraction of 1, one litter had a survival fraction of 2/3 and seven had a survival fraction of 0. These 11 values have exactly 1320 distinguishable permutations (multinomial coefficient). We based the exact permutation tests in our statistical analyses on these 1320 permutations.

Bear Blk's litters had a survival probability of 0.67, compared with 0.21 for all other mothers averaged together (raw survival rates, uncorrected for salmon or for play). Blk's litters also played more than those of other mothers (2.9 *vs* 1.9% of the time). But neither survival ($P = 0.364$) nor play ($P = 0.713$) differed significantly between Blk's families and the families of other mothers. The two-sample unpaired randomization test (Conover, 1999) used here has statistical power of about 0.4 for the observed difference in raw survival. The chance of detecting a real difference in survival as large as or larger than that observed is between one chance in three and one chance in two.

Our average ratings of cub body size, physical robustness and activity (three hypothesized components of overall condition) strongly predicted average condition (linear fit through the origin, $F = 234.1$, $P < 0.001$, multiple $R^2 = 0.99$). Activity ($t = 5.5$, $P = 0.0006$) and robustness ($t = 3.1$, $P = 0.02$), but not body size ($t = 0.52$, $P > 0.10$), contributed significantly to the fit of the linear model.

Activity measures based on direct behavioural observation agreed with our averaged activity ratings ($r^2 = 0.39$, $P = 0.03$).

Survival appears to increase as play increases (Fig. 1). Condition, fish and play together predict survival (Table 1). Increased play still implies increased survival (Fig. 2) (partial $r^2 = 0.49$, $P = 0.014$) after partialling out fish and cub condition. No measure of mothers' individual distinctiveness can explain variation in survival or in play (Table 2), adjusting for condition and fish.

The full model of survival has three predictors. A concise two-predictor model including condition and play, but not fish, has virtually all the explanatory power of the full model (Table 1). In the concise model, partialling out cub condition, survival increases as play increases (Fig. 2) (partial $r^2 = 0.30$, $P = 0.048$). No measure of mothers' individual distinctiveness can explain variation in survival or in play in the concise model (Table 2), adjusting for condition.

We conducted separate sensitivity analyses of the full (three-predictor) regression model and of the concise (two-predictor) regression. Assuming no more than 25% relative error in predictors, both the full and concise linear regression models appear very robust to possible observation errors in predictors (Appendix 2). The chance that our results were influenced by observation errors in the predictors is quite small.

No data point had a Cook's distance of more than 0.21 for the full model. No data point had a Cook's distance of more than 0.26 for the concise model. These results indicate that no single data point unduly influenced the fit of either model to the data.

Cook's distances for Blk's three litters were 0.01, 0.06 and 0.21 (mean 0.09, median 0.06) for the full model and 0.04, 0.14 and 0.26 (mean 0.15, median 0.14) for the concise

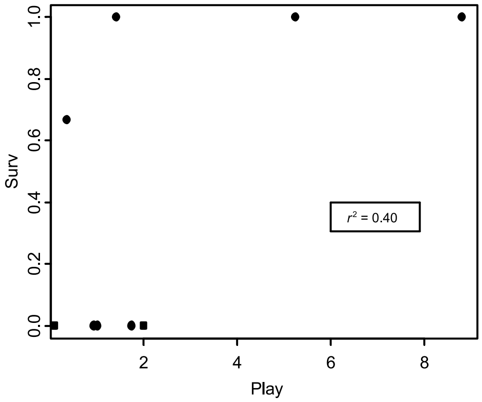

Fig. 1. The relationship between first-year survival and play. Unit = litter, $n = 11$. Filled squares represent two litters with identical or near-identical values.

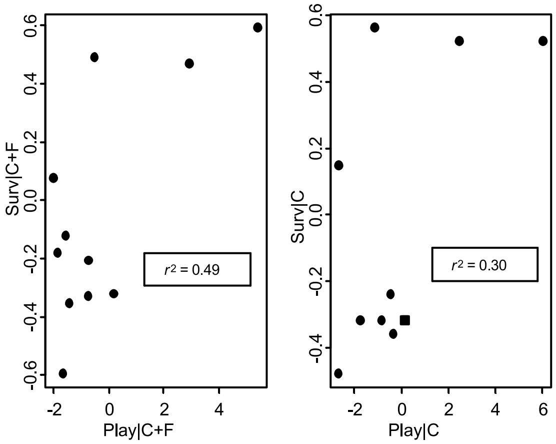

Fig. 2. The relationships between first-year survival and play in the full linear model (Surv|C + F, Play|C + F), given cub condition (C) and salmon availability (F), and in the concise linear model (Surv|C, Play|C), given cub condition. Unit = litter, $n = 11$. Filled squares represent two litters with identical or near-identical values.

model. Cook's distances for all other litters had mean 0.06, median 0.04 for the full model and mean 0.05, median 0.03 for the concise model. Cook's distances for Blk's litters did not differ significantly from those of other mothers' litters for the full model ($P = 0.51$, two-sample unpaired randomization test) or for the concise model ($P = 0.08$, two-sample unpaired randomization test).

Results from logistic regression analysis of survival in response to condition, fish and play do not differ substantially from those found by linear regression (Table 3). Logistic and linear regression models predict similar values for survival: $r^2 = 0.81$ for the full models and 0.68 for the concise models.

Table 1. Multiple linear regression models of juvenile survival

	Full model	Concise model
F (d.f.)	8.7 (3,8)	8.5 (2,9)
P	0.019	0.022
r^2	0.77	0.65
Residual standard error (S.E.)	0.32	0.36
Regression coefficient for condition (± S.E.)	0.18 ± 0.075	0.06 ± 0.05
Partial correlation coefficient for condition	0.64 ($P = 0.061$)	0.41 ($P = 0.088$)
Regression coefficient for fish (± S.E.)	−0.0027 ± 0.0014	—
Partial correlation coefficient for fish	−0.56 ($P = 0.091$)	—
Regression coefficient for play (± S.E.)	0.12 ± 0.04	0.09 ± 0.05
Partial correlation coefficient for play	0.70 ($P = 0.014$)	0.55 ($P = 0.048$)

Note: P-values from permutation test.

Table 2. Correlations of adjusted survival with maternal factors

	Full model	Concise model
PC1	0.01	0.06
PC2	0.52	0.40
z_1	0.18	0.03
z_2	0.32	0.24
z_3	−0.26	−0.26
z_4	−0.17	−0.12

Note: PCi = principal component i; $z_i = z$-score factor i. None of these correlations is statistically significant ($P \geq 0.09$ in each case). Randomization test with 5000 replicates.

Table 3. Logistic regression models of juvenile survival

	Full model		Concise model	
Predictor	Coefficient (± S.E.)	P	Coefficient (± S.E.)	P
Condition	5.4 ± 1.5	< 0.001	4.6 ± 0.47	< 0.001
Fish	−0.025 ± 0.046	0.20	—	—
Play	3.4 ± 1.7	0.017	2.4 ± 1.2	0.017

Note: Full model fit: likelihood ratio test statistic = 12.4 on 3 d.f., $P = 0.0061$. Concise model fit: test statistic = 11.7 on 2 d.f., $P = 0.0029$. Tests of coefficients were χ^2 on 1 d.f.

DISCUSSION

Charles Darwin and Charles Elton both knew about play. They also considered its possible biological significance but reached few firm conclusions. Darwin (in Romanes, 1884, pp. 378–379) found play at best a trifling instinct. But in his notebooks, he also commented on play's importance for human biology (Gruber and Barrett, 1974, p. 281). Elton (1927, pp. 55–56), citing A.B. Percival's observations of black rhinoceros *Diceros bicornis* play (Percival and Cuming, 1924, p. 209), viewed play as a way of doing nothing. With neither evidence nor a mechanism linking play to ecology and evolution, biologists continued to find play enigmatic and even baffling (Martin and Caro, 1985; Caro, 1988).

Our results link increased play to increased short-term survival. We consider our conclusions novel and robust to errors in predictors and to details of fitting methods (linear *vs* logistic regression). Martin and Caro (1985) and Caro (1995) suggested that students of play consider short-term rather than long-term effects (benefits as well as costs), precisely the time-scale of our results. Fagen (1993) developed life-history models for play assuming short-term benefits and short-term costs. Martin and Caro saw little hope for detecting either costs or benefits of play, especially over time-scales of the order of a generation. But Caro (1995) and Sharpe *et al.* (2002) successfully measured short-term costs of play. To our knowledge, no previous field study has detected either short-term or long-term benefits.

The distinction between partial and total effects of play has statistical and biological meaning. The partial effect of play on survival, given the values of one or more conditioning variables, measures effects of play with all effects of the conditioning variables on play and on survival removed before analysis of play relative to survival. If, for example, play contributes to survival in ways that condition does not, and cubs in better condition play more, the effects of play *per se* will be removed from survival when the effects of condition are removed. If we adjust play and survival for the effect of condition on both variables, the effect of the additional play resulting from above-average condition will show up statistically as a condition effect, rather than as a play effect. For this reason, adjustment of play and survival for maternal variables may prove overly conservative. Such adjustment surely underestimates the true importance of play for enhanced survival.

Our measure of salmon availability varies appropriately among years. However, it does not index variation in salmon consumption among individuals in a given year. The negative regression coefficient for salmon availability in the full model agrees with expectation for a predictor in multiple linear regression that has no significant effect on the response. We feel that the measure of condition that we used reflects several important effects of salmon consumption by mothers in prenatal and natal years and by cubs during their natal year, including effects of mothers' salmon consumption on mothers' lactation.

Our sample of 11 litters results from 10 successive years of field study. It includes all bear families observed sufficiently frequently for analysis, a total of 19 cubs. Our study amounts to a census with near-complete coverage. But to what extent are our conclusions, though apparently promising, still vulnerable to the realities of small sample size?

We recognize two primary concerns with small samples. Predictor variables may include chance error. And particular cases (e.g. a single highly sensitive, skilled mother, like the chimpanzee, Flo, that Jane Goodall studied) can potentially influence results and conclusions.

We used two kinds of sensitivity analysis to ensure that our results were not vulnerable in a statistical sense to errors in predictor variables or to particular litters with an unusually large or small amount of play. We used Chambers' method and Cook's distance to show that our models, and therefore conclusions based on them, were robust to measurement error in predictor variables and to possible influence of individual cases. No single mother influenced our results excessively. The two litters with the most play were offspring of two different mothers in two different years: bear Blk in 1987 and bear S in 1985.

Relative to other Pack Creek and Admiralty Island females (Taylor *et al.*, 1984; Schoen *et al.*, 1987), bear Blk was a successful mother. A relatively long reproductive lifespan and a relatively high annual birth rate explain her superiority. Her cubs' chances of survival also seemed higher, though not significantly so. This difference, even if real, could easily reflect salmon, play or both, not maternal effects. Still, the apparent difference in raw survival rates between Blk's litters and the litters of other mothers might immediately suggest maternal effects to biologists whose outlook posits maternal effects as the most parsimonious hypothesis *a priori*. Recognizing this view, we saw need for more thorough analyses. We therefore identified maternal characteristics and factors that might hypothetically affect offspring survival. Our analyses of these maternal characteristics and factors indicate that maternal effects alone do not account for our results.

Our ratings of mothers' individual distinctiveness (Fagen and Fagen, 1996) and our overall impressions of Blk and of other mothers in the study leave little doubt in our minds that brown bear mothers at Pack Creek do indeed contribute to the well-being and survival of their offspring. Mothers can help their offspring survive through play, through provisioning and protection, and through the overall emotional quality (Hinde, 1979) of the mother–offspring relationship.

Survival may increase non-linearly as play increases (Fig. 2), with diminishing returns at higher play frequencies. Statistical confirmation of non-linearity would be difficult with only 11 observations. The non-linear pattern evident on all three plots makes biological sense. We used permutation and randomization tests that did not assume linearity or normality. Empirically, we can find transformations that produce linear or near-linear scatterplots, for example $x = (2.5 + \text{Play}|\text{Condition})^{1/3}$, $y = (\text{Survival}|\text{Condition} - \min(\text{Survival}|\text{Condition}) + 0.01)^{3/2}$. The forms of these transformations have no particular biological implications other than that they capture the non-linearity of the scatterplots. Statistically, linear models perform well in comparison to non-linear models. And linear fits effectively detect overall trends in data (e.g. analysing $y = x^2$ data with the model $y = x$ for x non-negative but not excessively large). An analysis of transformed data might produce stronger correlations and higher significance levels. But its biological conclusions would almost surely mirror those reported in this paper.

Our findings raise two sorts of biological questions. First, if play increases short-term survival, how might populations of animals respond over demographic and over evolutionary time-scales? Second, what mechanism or mechanisms might link play to short-term survival?

Admiralty Island brown bears, other ursids (e.g. the polar bear *Ursus maritimus* and the giant panda *Ailuropoda melanoleuca*) and other mammalian (e.g. anthropoid apes) and avian species (e.g. large parrots, ravens) have 'slow' life histories (Gaillard *et al.*, 1989). Both in absolute terms and for a given body size, these species have long interbirth intervals, mature late and have small litters relative to those of other mammals and birds. This complex of life-history traits generally accompanies prolonged parental care and involves factors (e.g. learning) that promote survival of individual young (Gould, 1977; Clutton-Brock, 1991). In the few mammalian species examined to date, play appears most frequent at ontogenetic stages of high neural plasticity (Byers and Walker, 1995; Fairbanks, 2000).

In mammals and birds with 'slow' life histories, population growth and individual fitness depend most strongly on infant and juvenile survival (Oli and Dobson, 2003). This result is theoretically and empirically robust. It incorporates particular life-history characteristics of mammals and birds as well as previous theory (Pereira and Fairbanks, 1993; Wachter and Finch, 1997; Altmann and Alberts, 2003). If play can increase survival of immatures, these life-history considerations may help explain the greater prevalence and perhaps even the greater elaborateness of play in orders of mammals and birds with 'slow' life histories (Fagen, 1981; Pellis and Iwaniuk, 1999). If possible, it would be interesting to seek to distinguish between brain size as a direct predictor of play and brain size as a correlate of both play and 'slow' life histories.

Long-lived, large-bodied, large-brained, slowly reproducing species whose populations tend to be relatively small pose challenging difficulties when particular hypotheses require large sample sizes and individually identified animals. But demonstrable ecological links and evolutionary connections between play and survival appear most likely in precisely these species.

Our findings shed no light on mechanism. They do, however, suggest that mechanisms by which play might influence fitness might be sought in pre-adult ontogeny. Such mechanisms may prove specific to the infant and/or juvenile stages of development (e.g. Martin and Caro, 1985). Enhanced stress resistance and enhanced neuromuscular performance are two highly plausible short-term benefits. Long-term benefits, possible in theory, may prove relatively difficult to demonstrate and to measure (Martin and Caro, 1985).

During late fall, winter and early spring, many putatively stress-related factors, including disease, death from hypothermia and malnutrition, are possible causes of cub mortality. Den flooding during thaws will further increase overwinter mortality (Schoen *et al.*, 1987). Future studies relating play to fitness might consider mechanisms by which play experience could enhance juvenile survival by improving cubs' stress resistance (Frederickson, 1998; Biben and Champoux, 1999). Behaviour, cognition and the nervous, endocrine and immune systems interact (e.g. Sapolsky, 1992; Ader *et al.*, 2001). Gregory Bateson, one of the first biologists to discuss play (Bateson, 1955, 1956), proposed an evolutionary model (Bateson, 1963) linking stress responses to somatic change in evolution. Biben and Champoux (1999) demonstrated unequivocal relationships between increased play and lowered cortisol concentrations in *Saimiri*. Despite these findings, past discussions of play have not considered psychoneuroimmunology, and psychoneuroimmunologists do not recognize play behaviour. But it makes sense to consider play as a context for rehearsing stressful situations and for recovering from stressful experiences. Play involves both control and loss of control, both predictability and unpredictability, both novelty and familiarity (Fagen, 1981; Sutton-Smith, 1997; Power, 2000; Spinka *et al.*, 2001). Interestingly, these three psychological dimensions are also essential for understanding the biology of the stress response (Sapolsky, 1992). Future theoretical treatments of play behaviour and stress should also consider not only benefits but also costs (Bateson, 1963; Barnard and Behnke, 2001; Bonneaud *et al.*, 2003) of immune responses and of stress responses in general.

Our findings suggest a relatively immediate cost–benefit trade-off strategy for play in the life history, contrary to the view that play, considered as preparation for adulthood, implies immediate costs and delayed benefits. Lifetime fitness depends in part, sometimes most strongly, on juvenile survival. Animal play could increase short-term survival, a major component of fitness in mammals and birds with 'slow' life histories. But other fitness components could have compensatory effects (cf. developmental equifinality; Bateson and Martin, 2000).

Our results also suggest novel opportunities for analysing and for interpreting extant field data. Many long-term behavioural studies of known individuals collect data on play, on survival and on factors that potentially affect both play and survival. Field studies of reproductive success may sometimes gain explanatory power if they also consider play behaviour as a potential component of pre-adult survival. Residual variation in early survival in some vertebrate populations may well be explained, at least in part, by unrecorded or unanalysed play events. Play may be correlated with other components of fitness, so that (absent experimental manipulation) statistical partialling out of effects in field data may be necessary to identify components of reproductive success that actually operated in particular field situations under study.

We feel that more studies of this sort need doing. More secure conclusions will emerge when other individuals like Blk and S are found, and when additional populations and species are examined. Whether based retrospectively on existing data or prospectively on studies yet to come, measurement of short-term effects on life-history variables offers a pragmatic approach to the functions and evolution of animal play.

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APPENDIX 1: MOTHERS' BEHAVIOURAL DISTINCTIVENESS – CHARACTERISTICS AND FACTORS

We rated 21 reliable characteristics (Fagen and Fagen, 1996): careless, conceited, confident with bears, curious about other bears, curious about people, curious about surroundings, devious, expert at fishing, flamboyant, gregarious with other bears, grumpy, has an attitude, hostile towards other bears, impulsive, insecure, irritable, nosey, show-off, solitary with respect to other bears, sparkly, stodgy.

Using z-scores, we identified four groups of individual characteristics, or 'factors'. Individual characteristics in each group were significantly associated with each other, but not with factors in any other group. Each factor based on z-scores was associated ($r \geq 0.7$ in absolute value) with one or more factors based on principal components. The first factor identified using principal components was similar to the fourth factor identified using z-scores ($r = -0.92$) and less strongly associated with the first and second z-score factors ($r = -0.82$ and -0.77, respectively), and the second factor from the principal components analysis was associated with the third z-score factor ($r = -0.72$). For completeness, however, the analyses of individual distinctiveness reported in the text included both z-score and principal component factors. We would expect results of the two approaches to be very similar and conclusions based on them to be similar or identical. The first two principal components together explained 74% of the variation in the ratings and were associated with all four factors based on z-scores. The first three principal components together explained 87% of the variation in the ratings. The first two principal components seemed to summarize most of the meaningful information in the ratings of individual mothers. The first principal component is a composite of curious about bears, curious about people, has an attitude and nosey ratings, with smaller contributions from most other characteristics rated. The second contrasts insecure and solitary with respect to other bears with confident with bears and expert at fishing.

APPENDIX 2: ESTIMATED MODEL SENSITIVITY TO ERRORS IN PREDICTORS

Measurements of the three predictors that we used include some amount of chance error. We needed to rule out the possibility of ill-determined models – that is, models in which one predictor was approximately equal to a linear combination of the others. Chambers (1992) presents a mathematical approach to assessing possibly ill-determined linear statistical models. His approach invokes theoretical results about numerical linear least-squares solutions, in particular the theory of singular value decomposition of a matrix of predictor values. First, Chambers calculates a scaled predictor matrix that represents the uncertainty or measurement error in the observed values of the predictors. Next, he determines the singular values of the scaled predictor matrix and examines these singular values systematically. Any singular value substantially less than the square root of the number of observations indicates that the linear combination of the original predictors corresponding to this singular value is essentially noise, under the assumptions about errors in predictors, and should not be included in a regression model of the data.

We applied Chambers' method to the matrices of predictors for our full and concise linear regression models, assuming relative errors of 25% or less in the predictor values. The full model has singular values of 48.2, 17.8 and 5.5. The concise model has singular values of 41.9, 9.9 and 3.3; the square root of the sample size is less than each of these values. These numerical results indicate (Chambers, 1992) a model robust to relative errors of 25% or less in predictor values. Both the full and the concise models have statistical meaning and neither appears ill-determined.