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Play behaviour and multi-year juvenile survival in free-ranging brown bears, *Ursus arctos*

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ABSTRACT

Background: Previous analysis suggests that brown bear play behaviour can enhance first-year survival.

Question: Can play behaviour enhance multi-year survival?

Organisms: Young brown bears (*Ursus arctos*).

Times and places: 1985–1994, Pack Creek, Admiralty Island, Alaska, USA.

Method of analysis: Regression models and diagnostics; principal components analysis.

Conclusions: Young bears that played more were more likely to survive to independence. This association did not result solely from condition, litter size, salmon availability, or maternal characteristics.

Keywords: Alaska, behavioural adaptability, behavioural flexibility, brown bear, facultative decisions, innovation, inter-subjectivity, life histories, mother–young relationships, plastic behavioural responses, play behaviour, pre-adult survival, *Ursus arctos*.

INTRODUCTION

Play behaviours abound in mammals and birds (Fagen, 1981; Burghardt, 2006; Pellis and Pellis, 2009). Frequent and complex play distinguishes mammalian orders whose members have large brains relative to body size (Iwaniuk *et al.*, 2001). Play is possible, perhaps even likely, in some reptiles and in some fishes (Burghardt, 2006). Octopuses, which are large-brained invertebrates, play with objects (Mather and Anderson, 1999; Kuba *et al.*, 2006).

Economic models (Fagen, 1981) argue, and some field data (Harcourt, 1991; Sharpe *et al.*, 2002) suggest, that play has biological costs. The benefits of animal play remain largely hypothetical (Caro, 1988; Sutton-Smith, 1997; Pellis and Pellis, 2009). But if play *per se* improves survival, growth, and/or reproduction, then play must be biologically beneficial, whatever the mechanism. Here we examine possible links between play and survival to independence in young, free-ranging brown bears.

We encourage others to seek possible play–survival covariation, especially in long-term field data. Relatively rare, large-bodied, large-brained, slowly developing animals have long interested behavioural biologists. But data on such species accumulate slowly. Can anything

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of interest be learned from relatively small samples of behaviour, the sort of information that a 10- or 20-year observational study of a community consisting of one or two dozen individuals might produce? Indeed, simple, robust methods, such as linear regression used with appropriate diagnostics (e.g. Fagen and Fagen, 2004), can allow statistical inference from relatively few cases. Working scientists rightly resist drawing general conclusions from a single study, no matter how highly significant the results in a statistical sense. But if more and more independent studies of a problem draw similar conclusions based on statistically significant results, although sample sizes for each study are (necessarily) small, we will have gained something.

We also seek to spur further thought on the developmental and evolutionary significance of play. Not all differences in play between classes of individuals or of species are necessarily adaptive. But students of play have posited multiple potential benefits over multiple time scales (e.g. Fagen, 1981; Bateson and Martin, 2000, pp. 182–197; Spinka *et al.*, 2001; Bateson, 2005; Burghardt, 2006; Pellis and Pellis, 2009; Lee and Moss, in press). Relatively short-term neuromuscular, neuroendocrine, and immunological improvements may result from play, helping individuals that are still immature to avoid predation and disease and/or counteract the effects of stress. Adults may also benefit in these ways or in others from playing as immatures. Play could increase behavioural variability and help calibrate and tune adaptive behavioural flexibility (Fagen, 1981, pp. 350–355; Bateson, 2005; Pellis and Pellis, 2009). Play may even assume a macro-evolutionary role as a mechanism for achieving what Gould (2002, p. 1214) termed the 'best possible balance between optimization for the moment and flexibility for future change'.

Individual condition, food availability, and differences among mothers all influence survival of immatures (Clutton-Brock, 1991; Wachter and Bulatao, 2003). But might survival also depend on play? Play can reduce survival probabilities by using energy (Sharpe *et al.*, 2002) and by increasing risk (Harcourt, 1991). Nevertheless, play's net effect on survival might be positive. We recognize, of course, that multiple causes are the rule in evolutionary ecology. Our approach will be to examine play simultaneously with other key biological variables that might also affect survival.

A link between play and biologically significant phenotypic (including developmental) adaptability would be constructive. It would connect the biology and natural history of play with the study of facultative decisions and plastic responses in evolutionary and behavioural ecology. Assessing rates of adaptation to environmental change (e.g. Lee, 1991), including global climate change (Visser, 2008), is a problem for biologists. In the light of current theory about play and behavioural adaptability, a suspected link between play *per se* and survival would be interesting in this context. It would enhance the scope of theory and would suggest new approaches to proximate and ultimate mechanisms of adaptation to environmental change.

METHODS

We observed individually identified, free-ranging brown bears, *Ursus arctos*, at Pack Creek, Admiralty Island, south-eastern Alaska (Post, 1982; Warner, 1987) in July–August 1985–1994 (Fagen and Fagen, 1996, 2004). In each of our 10 successive annual field seasons, observers spent at least 600 h on site, using focal-animal sampling methods to estimate the percentage of time each individual spent playing. Focal samples sought to allocate roughly equal sampling effort to each family when in sight, so that a few particularly playful families would not end up dominating the data.

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 to determine that a bear was playing. These criteria included the silence of play (in contrast to the loud vocalizations associated with aggressive displays and with escalated fights), the brown bear play-face or relaxed open-mouth grin, and a characteristic, transverse planar rotation of the upper torso initiated in the upper back and resulting in elevation of the foreleg on one side of the body.

We identified ten individual mother bears. As a group, these ten mothers had 14 families of 1–3 cubs each. Thirteen of these families (nine mothers, 24 young) were each observed for 15 h or more before the juveniles' nutritional and spatial independence from their mothers at the beginning of their third (6 surviving young) or fourth (5 surviving young) summer (Table 1). We observed no actual mortality. When young did not return with their mothers and were not observed during the year following their birth, they were assumed not to have survived. Young bears did not become independent before at least their third summer. Dispersal (chiefly of males) out of the study area was gradual and infrequent and occurred one or more years after independence. For these reasons, dispersal out of the study area would not be expected to affect our assessment of survival to independence. We defined multi-year survival as the percentage of each litter of cubs-of-the-year (spring cubs) surviving from the first week of July of their natal year to independence when observed in the first week of July of their third or fourth year.

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. These estimates, based on aerial and on on-the-ground field surveys in 1985–1994, are well established, reliable, and sufficiently precise for the management of salmon runs (Groot and Margolis, 1991; Heinl *et al.*, 2004; Zadina *et al.*, 2004). We defined salmon availability as 'pink numbers + 3 times chum numbers', which reflects species differences in average weight (a chum salmon returning to

Table 1. Data for the study

Family	Mother	Survival to independence	Condition	Play	Fish$^{1/2}$	Birth year	Maternal influence
bi	Bki	2/3	4	2.2	92.0	1987	1.46
kdl	Blk	2/2	4	4.0	87.4	1987	1.47
kaw	Blk	1/2	4	1.4	87.3	1990	1.47
g1	Blk	0/1	3	2.0	195.3	1994	1.47
b1	Brn	0/1	3	2.0	86.9	1988	0.92
ndl	N	0/2	4	0.10	69.5	1991	0.00
nc	NF	0/1	3	0.12	69.5	1991	−0.40
paw	P	0/2	3	1.0	83.4	1990	1.50
q12	Q	0/2	2.5	0.94	83.4	1990	0.70
r1	Q	0/1	3.5	1.8	195.3	1994	0.70
sj	SJ	2/3	4.5	2.0	141.3	1985	1.47
sdl	S	2/2	4	5.4	148.2	1985	1.00
mdl	Bki	2/2	4.5	0.56	80.7	1991	1.45

spawn weighs roughly three times as much as a returning pink salmon) (Groot and Margolis, 1991). Salmon values were summed over all years during which a young bear depended on its mother. To these values we added the salmon value for the year before the young bear was born. By doing so, we sought to include possible effects of pre-natal salmon availability on maternal nutrition. In this paper, 'fish' will denote this aggregate measure of overall salmon availability and $\text{fish}^{1/2}$ its square root.

Ratings

We assessed young bears' condition by rating (Hinde, 1979; Feaver *et al.*, 1986; Fagen *et al.*, 1997) each of the 13 litters on a scale of 1 to 5. We averaged our results to yield an overall condition score for each litter [Kendall's *tau* for observers' independent ratings = 0.48, $P = 0.011$, $n = 13$, exact test allowing ties (Conover, 1999, pp. 319–323)]. Our average ratings of body size, physical robustness, and activity – three hypothesized components of overall condition – strongly predicted average condition (linear fit through the origin, $F_{3,9} = 702.8$, $P < 0.001$, multiple $R^2 = 0.99$, $n = 13$). Activity ($t = 6.0$, $P = 0.0001$) and robustness ($t = 3.1$, $P = 0.01$), but not body size ($t = 0.77$, $P > 0.10$), contributed significantly to the fit of the linear model. We verified the validity of our activity ratings by comparing them with activity data from our field study. A behavioural measure of activity – the difference between percent time in sight spent travelling or fishing and percent time in sight spent waiting while mother fished or rested – agreed with our averaged activity ratings ($R^2 = 0.32$, $P = 0.04$, $n = 13$).

We rated each of the nine mothers on six individual characteristics: *careless*; *confident with bears*; *curious about other bears*; *curious about surroundings*; *expert at fishing*; and *insecure* (definitions in Fagen and Fagen, 1996). Two independent observers had agreed reliably on these and 15 other characteristics ($r \geq 0.70$) in a previous study of individual distinctiveness in Pack Creek brown bears (Fagen and Fagen, 1996). From these 21 characteristics, we chose those six that varied among mothers and that also had obvious potential for influencing young bears' well-being and survival. Mean ratings by the two observers of each of these six reliable characteristics on a scale from 0 to 1 served to define our measure of maternal influence, an overall predictor of offspring survival to independence based on maternal behaviour, as follows: *careless* and *insecure* were considered potentially deleterious to survival and the other four characteristics as potentially aiding survival.

Data analysis

We treated each litter as a sampling unit. Six of nine multiple-cub litters either survived or did not survive as a whole. For this reason, although all observations were on individuals, it would not have been appropriate to use individuals as sampling units in a study of factors affecting survival. None of the four single-cub litters survived. We defined survival as the fraction of a litter's young that survived from the beginning of the field season in their natal year to the beginning of the field season in the first year a juvenile was consistently observed moving and feeding independently from its mother. Three of the 13 survival fractions were equal to 1; two were equal to 2/3; one was equal to 1/2; and seven were zero (Table 1). In a given multiple-cub litter, all surviving littermates became independent at the same age.

We used linear statistical models (Chambers, 1992; Neter *et al.*, 1996). Logistic regression would have been inappropriate because it is strictly a large-sample method. Logistic regression's model-fitting and inference methods are valid only for large samples and can even be unstable numerically for small samples. Log-linear analysis of contingency tables would also have required larger samples – a miminum of 2–5 observations per cell (Bishop *et al.*, 2007). A three-way table with 8 cells – 'low' and 'high' values for play, for condition, and for survival – would therefore have required 16–40 observations per cell.

We built and compared multiple linear regression models of survival. We used least-squares fits. Our play measure was percent time in sight spent playing, averaged over all young in a litter. For each litter, we calculated a play value as the overall average play frequency (percent time in sight) for all littermates, where each littermate's average included all years of observation for that individual. We transformed overall salmon availability (square root transformation) as is customary in data analysis for non-negative quantities that vary over several orders of magnitude and have right-skewed empirical distributions (Neter *et al.*, 1996, p. 126).

We summed an individual mother's rating on the four 'likely beneficial' personality characteristics (see above) and then subtracted the sum of that individual's ratings on the two 'likely deleterious' characteristics from that total to get each individual mother's influence measure. The maximum possible value for this measure was therefore 4 and the minimum −2. Values recorded ranged from 1.47 to −0.4.

Multiple regression models should be as simple as possible. They should use well-chosen predictors that are sufficient to explain most variation in the data. We first examined pair-wise scatterplots of the possible predictors to identify possible simplifications. The only strongly associated predictors were litter size and condition ($R^2 = 0.36$, $P = 0.023$). No other correlation among predictors was statistically significant. The first principal component of litter size and condition explained 80% of variance in these two predictors. We used this first principal component, designated LC, as a predictor in our regression models.

To assess the overall fit of a model to the data, we tested the multiple correlation coefficient by calculating its value for each of 10,000 independent random permutations of the survival values regressed on the same predictor values, and then comparing the resulting correlations with the actual value. (Equivalent randomization tests on the overall F-statistic for the model would have yielded the same results.)

We used linear regression to remove effects of other variables from both survival and play. We then calculated product–moment (Pearson) partial correlations (Neter *et al.*, 1996) of survival and play adjusted for the other variables. We used sampled randomization tests (Edgington, 1995) with 10,000 replications to assess statistical significance of partial correlation coefficients. A negative correlation of play with survival would be equivalent to failure to reject the null hypothesis of no enhancement of survival by play. Accordingly, we used one-sided tests to assess the statistical significance of play in relation to survival.

Initially, we defined a 'full model' as one that used play, LC, fish$^{1/2}$, and maternal influence to predict survival. To simplify the full model, we sought one or more models that had fewer predictors than the full model but that retained essentially all its ability to predict survival. We used C_p-diagnostic values (Chambers, 1992; Neter *et al.*, 1996) to identify simpler models that used subsets of the predictors. We plotted C_p for each possible regression model against p, the number of parameters in the model (p = number of predictors plus 1 for the intercept). Models for which the C_p-value is small and also near p have small random errors and small bias errors. The most attractive model with exactly p parameters would be the model whose C_p-value is closest to p. The $(p - 1)$ predictors in this model then define a desirable, concise model.

To confirm that a concise model identified using C_p had virtually all the predictive power of the full model, we used a randomization test on multiple-partial *F*. This test calculated the statistical significance of the difference between full and concise models.

To analyse sensitivity of linear regression fits to possible uncertainties in the predictors, we used scaled predictor values (Chambers, 1992). This approach requires estimates of actual errors in predictors. We assumed a relative error of 25%, almost surely an overestimate in view of the total hours of behavioural observations and the fact that salmon abundance estimates involved replicated aerial and on-the-ground surveys by experienced observers. The resulting error estimates were 0.5% for play frequencies, 0.17 for LC, 25 for fish$^{1/2}$ (equivalent to 625 for fish), and 0.5 for maternal influence. We divided the predictor values by these uncertainty values to define scaled predictor values. We then computed singular-value decompositions (Golub and van Loan, 1989) of the predictor matrix.

Diagnostic plots and Cook's distances (Neter *et al.*, 1996) were used to detect influential outliers and/or possible non-linearities that might compromise the linear least-squares fits. The Cook's distance associated with an observation measures the influence of that observation on the overall regression.

We used partial regression plots (Neter *et al.*, 1996) to identify families in which young gained large survival benefits from play *per se* and families in which young incurred large survival costs from play *per se*. A partial regression plot displays the specific effect on the response of one predictor in a regression, with all effects of the other predictors removed from both the selected predictor and the response.

We used the *S-Plus 2000 for Windows*® data analysis system (Insightful Corp., Seattle, WA), with default values for all analyses.

Possible general statistical concerns about field data on individual behaviour might include sample size, non-independence, temporal autocorrelation, survival data biased by age differences in play frequencies, and possible effects of maternal experience (i.e. litter survival for primiparous mothers vs. multiparous mothers). To guard against such concerns, we omitted two additional families for which we felt observation time was insufficient; we chose appropriate sampling and data analysis methods; and we sought adequate models that had as few parameters as possible and did not over-fit the data. Furthermore, we considered the following additional possible sources of error.

Most litters survive or do not survive as a whole. Similarly, littermates' play frequencies are similar because so much play occurs between littermates. For these reasons, we used the litter, rather than the individual, as the unit of our analyses (although actual data were originally collected on individuals).

We paid particular attention to possible statistical implications of age differences in play frequencies. If play rates before independence vary only slightly with age, no bias will result. But if young play more in their first year, then survival and play would appear to be negatively associated because the survivors would play less during their second (and third, if applicable) summers. And if young play more after their first year, then survival and play would appear to be positively associated. Play of immatures generally decreases with age, and a sustained increase in play after the first year would be surprising. We compared play rates within litters across years for the young bears in this study. Play rates did not change significantly between the first and second summer of life [$P = 0.45$, $n = 6$ litters; randomization test for paired observations (Conover, 1999, p. 412)]. From the second to the third summer, changes in play rates for the three litters that remained with their mother for a third summer were −0.1%, 5.8%, and −0.5% respectively. Play rates for two litters born in 1984 changed

0.1% and −4.2% respectively from the second to the third summer. Second-summer and third-summer young still depending on their mothers seem to play at about the same rates. Overall, rates of play appeared not to vary with age. An absence of consistent age differences in play rates means that age did not bias the play-survival data.

A mother's previous experience, or lack of previous experience, in raising young can, in principle, affect survival of her litters. But no such relationship is apparent in our data. Of the 13 litters analysed, three were born to mothers whose previous reproductive history was not known. Seven litters were born to mothers who had been seen with cubs in previous years. And three litters were born to mothers who had been observed each year since they were juveniles and had never been seen previously with cubs. We analysed possible survival differences among these remaining ten litters in relation to mothers' known reproductive history (primiparous vs. multiparous). We found no differences in litter survival between primiparous and multiparous mothers ($P = 0.16$; two-sample unpaired randomization test analogous to Wilcoxon test). We do not deny that maternal experience can affect offspring survival in mammals, but we found no indication that such effects could have influenced our results.

RESULTS

Eleven of 24 young survived to independence. Survival appears to increase as play increases (Fig. 1). Survival fits a linear regression model that incorporates play, LC, fish$^{1/2}$, and maternal influence (Table 2). Increased play still implies increased survival (Fig. 2, left-hand graph) after partialling out fish$^{1/2}$, LC, and maternal influence (Table 2).

The full model of survival has four predictors and an intercept. A simpler model would be preferable. The best C_p-values for three-predictor models are 3.3 (play, LC, maternal

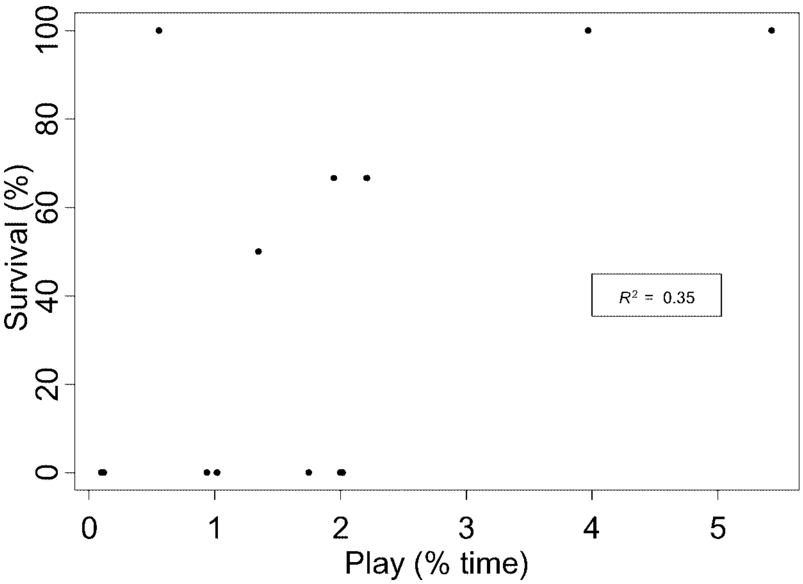

Fig. 1. The relationship between survival to independence and play in the raw data (Table 1). Unit = litter, $n = 13$.

Table 2. Multiple linear regression models of survival

Model	Full	Concise
F (d.f.)	7.1 (4,8)	28.4 (2,11)
P	0.01	0.0009
R^2	0.78	0.84
Residual S.E.	0.25	0.25
Regression coefficient for play (± S.E.)	0.15 ± 0.06	0.18 ± 0.03
Partial R^2 for play	0.45	0.44
P for play	0.0093	0.0096

Note: P-values from randomization test. Full model includes intercept. Concise model is without intercept.

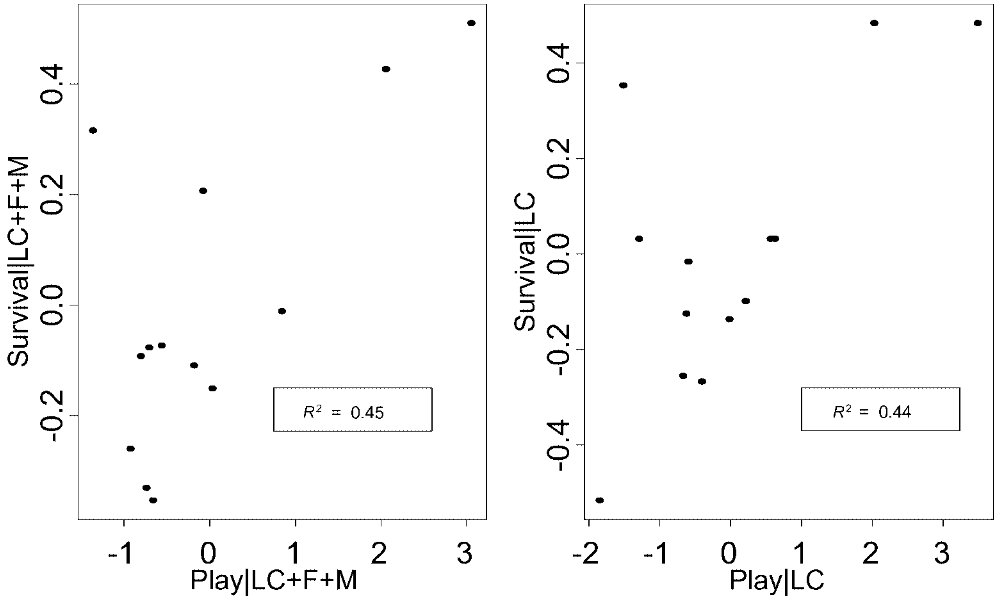

Fig. 2. Partial regression plots. The relationships between survival to independence and play in the full model (left-hand plot) and in the concise model (right-hand plot). LC = first principal component of litter size and condition, F = fish^{½}, M = maternal influence. Survival and play both adjusted for the effects of the other linear predictors: LC, F, and M in the full model, LC in the concise model. With these effects removed from both survival and play, the plots show the effect of play *per se* on survival, uninfluenced by the other predictors. Unit = litter, $n = 13$.

influence) and 4.0 (play, LC, fish^{½}). The best C_p-value for a two-predictor model is 2.1 (play, LC). The next best two-predictor C_p-value is 7.7, much higher. We chose the concise two-predictor model with play and LC but with no intercept. This concise model predicts survival almost as well as does the full model (Table 2). Concise and full models do not differ statistically (multiple-partial $F_{3,9} = 0.82$, $P = 0.52$). In the concise model (with LC partialled out), survival increases significantly as play increases (Fig. 2, right-hand graph; Table 2).

The full and concise models both appeared very robust to possible observation errors in predictors (Appendix). 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 0.45 for the full model. No data point had a Cook's distance of more than 0.25 for the concise model. These results indicate that no single data point unduly influenced the fit of either model to the data.

In the concise model, a 1% increase in time spent playing increased expected survival probability by 18% – nearly a fifth. Predicted survival without play versus with play varied among families, with some dramatic increases (Table 3, Fig. 3).

DISCUSSION

Play increases survival to independence. This conclusion stands even when we take all other factors considered (litter size, condition, fish, maternal characteristics) into account. We used linear least-squares regression with appropriate diagnostics. Our approach offers high reliability. The conclusion that play *per se* increases survival to independence did not vary across models. We found a desirable, concise regression model that was sufficient to represent the data using only two fitted parameters and no intercept. Both in the concise model and in the full model, play *per se* increased survival to independence significantly, with all

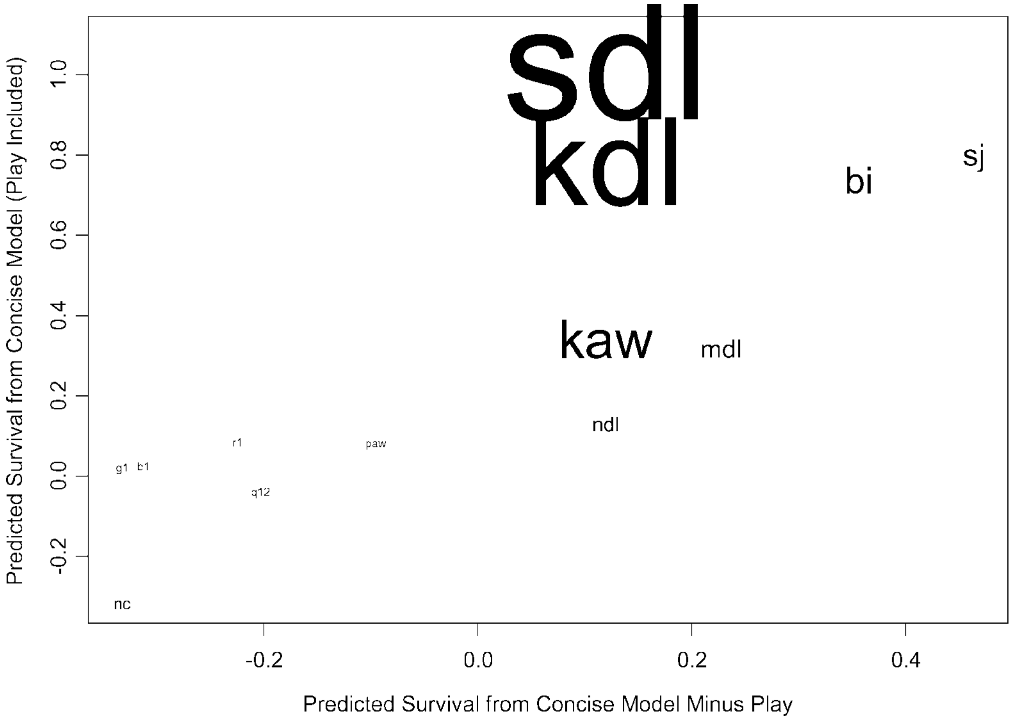

Fig. 3. Predicted survival with and without play included, concise model. Plotting symbols are the codes used to identify litters (Table 1). Size of plotting symbols proportional to ratios (play/no play) of predictions. Ratios corresponding to predictions of survival ≤ 0 plotted with very small characters for visibility.

Table 3. Predictions (concise model) of survival

Family	Without play	With play	Ratio with/without
bi	0.36	0.75	2.1
kdl	0.12	0.83	7.0
kaw	0.12	0.36	3.0
g1	<0	0.02	—
b1	<0	0.03	—
ndl	0.12	0.14	1.1
nc	<0	<0	0.9
paw	<0	0.09	—
q12	<0	<0	—
r1	<0	0.09	—
sj	0.46	0.81	1.8
sdl	0.12	1.09	9.1
mdl	0.23	0.33	1.4

other potential influences on survival controlled for statistically. The regression coefficient of play had near-identical values across models, no matter what other predictors were present – another strong indication that the hypothesized effect of play *per se* on survival holds for our data. This conclusion was also not affected by errors in predictors or by outliers.

Bears Blk and Bki had the most litters born (3 and 2 respectively), the most independent young surviving from these litters (4 and 4), and the longest reproductive lifespans (7 years and 4 years) of any mothers during the 10 years covered by our study. Both Blk and Bki also had additional offspring previously born and surviving to independence at Pack Creek. Overall, our subjective impressions of Blk, Bki, and other mothers at the site and our ratings of these mothers' individual distinctiveness (Fagen and Fagen, 1996) suggest, not surprisingly, that brown bear mothers at Pack Creek do indeed contribute to the well-being and survival of their young. We feel that our inclusion of an aggregate measure of maternal differences in the analysis helps to address possible concerns about non-independence.

We need further studies of this kind. Our key point is that statistical patterns in our data indicate a role for play *per se* in juvenile survival, both in survival to independence and during the first year of life (Fagen and Fagen, 2004). In our study, young bears that played more tended to survive best to independence. Our data support play as a survival factor. The data do not indicate what play contributes. The data only indicate that play makes its own contribution to survival, over and above obvious factors such as food, litter size, condition, and differences among mothers.

Our findings do not address the question of mechanism. They do, however, suggest that mechanisms by which play might increase survival might be sought in pre-adult ontogeny. Play may have particular benefits during particular stages of development (e.g. Martin and Caro, 1985). In other words, play is not necessarily practice for adulthood.

We did not observe any mortality during our field seasons. In all likelihood, brown bear pre-adult mortality results from events occurring during the stressful environmental conditions of winter hibernation and early spring. Exposure and infectious disease are two possible agents. In theory, play could produce a more resilient individual, capable of withstanding stress in ways that physical condition alone would not predict. In other populations or species, these same factors could still be important, but in different ways – in mediating development and performance of behaviours involving predator avoidance and defence, for example. Predator avoidance and defence necessarily involve cognition and emotion, whether the argument is made in physiological terms or in behavioural terms. Pellis and Pellis (2009, p. 73) suggest play helps rats 'refine the ability to deal with potentially threatening and stressful situations more adequately' (e.g. Potegal and Einon, 1989; Einon and Potegal, 1991). Why not hypothesize that play experience can impart emotional flexibility that would help decrease predation risk?

Pre-weaning survival is a component of lifetime reproductive effort, a key to fitness and a central concept in the study of life histories (Charnov *et al.*, 2007). Variation in age at independence among individuals might merit explicit theoretical consideration in life-history studies. It might lead to refined trade-off and production assumptions and to improved approaches to estimation, especially in species with 'slow' life histories (see, for example, discussion in Fagen and Fagen, 2004).

Longitudinal information on long-lived, slowly reproducing mammalian and avian species accumulates slowly. Field data that barely meet consensus criteria for sample size (say, 25–100 individuals or families, depending on the appropriate sampling unit) but include information on survival, play, and a few key predictor variables thought to be important for pre-adult survival are worthy candidates for analyses like those here. Linear regression methods are powerful, reliable, and largely robust to violations of assumptions, even in small samples. Appropriate analyses of several smallish data sets can yield much valuable information. This general principle of cross-validation can likewise be very effective when applied to a single large or even medium-sized data set.

If comparable conclusions emerge consistently from several independent data sets, such findings would be more than worthy of note. To discover what information might be present, one simply needs to do the analyses. Our results suggest novel opportunities for analysing and for interpreting extant field data. Many long-term behavioural studies of known individuals include data on play, survival, and factors that potentially affect both play and survival. Such long-term data sets should be excellent candidates for analyses similar to those reported here.

In a long-term behavioural study involving marked inter-annual variation, analyses of play and survival may need to consider the potential effects of the costs of play. Suppose that years are either good or bad, and that play rates vary among individuals both in good and bad years. Furthermore, make the plausible assumption that play is more costly in a bad year than in a good year. If costs of play in a bad year exceed benefits in that year, net play-induced survival to the next year may be less for those individuals that play more during the bad year. This effect might make it more difficult to detect positive effects of play, even if present, in a long-term study that included years of both types. On the other hand, during a bad year, play may not occur at all.

Play improves survival. But which individual bears benefited from play? That is, by playing more than average, which survived better than they would have otherwise? And which bears lowered their chance of survival by not playing often enough? Based solely on the data available, we cannot answer these questions conclusively. Nevertheless, we find the following results suggestive.

Young of the sdl and kdl families seemed to beat the odds. They survived far better than otherwise expected (sdl nearly nine-fold, 12–100%; kdl seven-fold, 12–83%). Other young (bi and kaw) also more than doubled their predicted survival (Table 3). Without play, predicted survival of the ndl family's young was also 12%. But their frequency of play (0.1%) was the smallest of any family studied. More play might have allowed survival of one or both young.

The mammalian family is a natural unit in considerations of individual and multi-level selection. Over macro-evolutionary time scales, climate change – in particular glacial and sea ice fluctuations – appear to have reshaped bear habitat and the history of the genus *Ursus*. Ideas about multi-level selection may prove relevant to interpreting parts of this history. We cannot rule out higher levels of selection as possible factors in the evolution of play behaviour across social groups and across vertebrate taxa.

The sdl, kdl, and mdl litters all became independent from their mothers a year early by Pack Creek standards – that is, at the beginning of their third summer. Each of these three sets of littermates stayed together during that summer. In laboratory experiments (Bateson *et al.*, 1990), weaning accelerates some forms of play in young domestic cats. Such play occurs after weaning begins. Play, social development, and age at independence also covaried in laboratory studies of rhesus macaques *Macaca mulatta* (Hinde and Simpson, 1975; Simpson *et al.*, 1981) and hooded rats *Rattus norvegicus* (Smith, 1991).

The following results might also be germane to our findings. Young bears may become independent a year early based on maternal age and condition and on the likelihood that the young will thrive on their own during their third summer. For example, young European brown bears in northern Sweden stay with their mothers for two or three summers (in one case, four). They tend to stay with their mothers for a third summer if their body mass as yearlings is relatively low. Keeping offspring for a third summer tends to compensate for low yearling body mass (Dahle and Swenson, 2003). Survival of the Swedish bears from ages 1 to 3 increased with increasing yearling body size (Dahle *et al.*, 2006). These studies used radio tracking and did not include systematic observations of behaviour.

Survival of newly weaned and independent young bears might also depend on individual resourcefulness and flexibility, ability to cooperate with each other and to co-exist with older bears, as well as on their chance of remaining on familiar ground, in their natal watershed. These benefits are precisely those most often hypothesized (generally, to be sure, without strong empirical evidence) for play: it could make animals more stress-resistant (Fagen and Fagen, 2004; Pellis and Pellis, 2009), behaviourally variable, flexible and innovative (e.g. Fagen, 1981; Spinka *et al.*, 2001; Bateson, 2005; Pellis and Pellis, 2009), able to adjust to new conditions (Lee, 1991), socially aware and attuned [e.g. inter-subjectivity and affect attunement (Stern, 1977, 1985, 2004; Malloch and Trevarthen, 2008)], and easier to live with (Ghiselin, 1982).

Field studies of reproductive success may gain explanatory power if they include 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 measure and to distinguish different components of reproductive success.

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APPENDIX: ESTIMATED MODEL SENSITIVITY TO ERRORS IN PREDICTORS

Our regression predictors include some 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 (0.5% for play, 0.17 for the first principal component of litter size and condition, 25 for fish$^{1/2}$, and 0.5 for maternal influence). The full model has singular values 17.6, 10.6, 5.3, 3.6, and 3.5. The concise model has singular values 17.5, 10.0, and 3.6. The square root of the sample size, 3.6, is not substantially greater than any 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 concise model have statistical meaning, and neither appears ill-determined.