

Captive fledgling American kestrels prefer to play with objects resembling natural prey

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Abstract. Object play may be a mechanism by which young predators acquire skills in manipulating prey, as well as physical strength and endurance. It has also been proposed that fledgling raptors play with live or dead prey if available, but would play with surrogates such as sticks or grass if not. Different objects were offered to captive fledgling American kestrels, *Falco sparverius*, to test whether they prefer to play with objects resembling prey. Individuals were divided into two groups: those in treatment A were offered mouse mimics, along with one of four objects (large and small pine cones, long and short twigs) which were alternated daily. Individuals in treatment B were offered bottle corks, and the same type of alternative objects as in treatment A. There were no significant differences in the mean number of play instances of birds in each of the two treatments (total of 506 instances). However, fledglings in treatment A played significantly more with the mouse mimics, whereas fledglings in treatment B played with the different objects in proportion to their availability. These results support the hypothesis that young raptors devote a relatively fixed amount of time to object manipulation, and that they prefer to manipulate objects resembling natural prey. The same set of objects were offered to adult American kestrels, but they were never manipulated. This suggests that object play has a function in the maturation of hunting skills of young raptors.

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Manipulation of inanimate objects, a frequent activity in young mammals, has also been observed in young and occasionally adult birds and has been regarded as object play (Fagen 1976, 1981; Ficken 1977). Manipulation of dead prey or objects such as leaves, twigs, sticks and stones has been reported in corvids, parrots and birds of prey, the avian groups where play is considered to be more prevalent (Fagen 1981). These manipulations usually take the form of tossing, pouncing and shaking the objects repeatedly, in the same way as young mammalian

carnivores play with objects (Fagen 1981). Dropping and retrieving objects in midair, or mock attacks on inanimate objects by raptors are also considered to be play (Sherrod 1983; Palmer 1988). Instances of social and locomotor play (for definitions, see Bekoff & Byers 1985) have been recorded in several avian species (e.g. Sherrod 1983; Blumstein 1990; Bustamante 1994), but object play seems to be the most frequently reported type of play in birds (Ortega & Bekoff 1987). Both free-ranging and captive individuals play with objects (Fagen 1981).

Descriptions of avian play are mainly anecdotal (Ortega & Bekoff 1987). Mueller (1974) studied prey recognition and predatory behaviour in captive American kestrels, *Falco sparverius*. He gave the kestrels a series of objects, ranging from a tissue-paper ball, a crude tissue-paper mouse, stuffed and dead mice, and also live mice. Attacks on the paper models were 'desultory and disoriented' and considered to be play rather than predatory behaviour. Attacks

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on live mice, on the other hand, were 'intense, rapid, sustained and well-oriented'. The paucity of studies on avian play contrasts sharply with the detailed observations and experiments available for both domestic and wild mammals (e.g. Fagen & George 1977; Bekoff & Byers 1981; Fagen 1981; Martin & Caro 1985; Gomendio 1988; Caro 1995).

Object play may be a mechanism by which young predators acquire skills in catching and manipulating prey (Mueller 1974; Ficken 1977; Fagen 1981; Sherrod 1983; Caro 1988), as well as physical strength and endurance (Fagen 1981; Bekoff & Byers 1985), or it may enhance the development of behavioural flexibility in young animals (Geist 1978; Fagen 1984; Ortega & Bekoff 1987; Wemelsfelder 1993). In fact, play seems to have evolved in species showing prolonged periods of parental care and it is mainly practised by juveniles (Bekoff & Byers 1985; Byers & Walker 1995).

Object play has been frequently observed in raptors that hunt agile and elusive prey, such as *Accipiter* and *Falco* species (Parker 1975; Sherrod 1983; Simmons 1984; Bustamante 1994), whereas more generalist feeders, such as *Milvus* kites, seldom play (Bustamante & Hiraldo 1989; Bustamante 1993). However, it is also possible that play with objects might occur only when young raptors do not have suitable prey on which to practise (Sherrod 1983). This hypothesis could explain why play with objects has been observed frequently by some researchers but never by others studying the post-fledging dependence period of the same species (Sherrod 1983).

We conducted an experiment to test whether captive fledgling American kestrels prefer to manipulate objects resembling their natural prey (small mammals, see Bird 1988) over other types of objects when offered both simultaneously in the absence of live prey. We hypothesized that young raptors devote some time to object manipulation to improve their hunting skills. Their actions will be predominantly directed to prey if available, but to other objects if not. Objects resembling natural prey should also be preferred over other types of objects. Additionally, we offered objects to adult kestrels to determine whether the tendency to manipulate objects was age-related.

Although not complete, this is the first experimental study of object play behaviour in birds and its relation to maturation of hunting skills.

METHODS

The study was conducted in 1994 at the Avian Science and Conservation Centre (McGill University, Canada), where over 300 American kestrels are maintained in captivity (Bird 1982). The individuals used in the experiment were reared by pairs in outdoor pens.

Each indoor test pen (2.5 × 1.5 × 2.5 m) had a front door with a one-way glass window (20 × 30 cm) for observations, a rear window (1 × 1.5 m) to facilitate natural temperatures and photoperiod, and a rope perch extending from side to side 1 m above the floor. The concrete floor of the pens was covered with wood chips. Individuals in one pen could not see individuals in other pens.

Experimental Design

Twenty-four fledgling American kestrels from six broods, aged 32–35 days at the beginning of the observations, were kept in groups of four birds (two males and two females) in six isolated test pens. American kestrels usually fledge (first flight from the nest) when 28 days old (Gard & Bird 1992; Negro et al. 1994), and thus the experiment started approximately a week after fledging. Individuals were sexed by plumage characteristics (Bird 1988), and 12 individuals of each sex were randomly assigned to treatment and pen. We identified individuals by painting the feathers around the tibia with water-fast markers. One male in treatment A escaped during the experiment and was not replaced. Thus, the final sample size was 11 birds in treatment A and 12 birds in treatment B.

We introduced into each pen a set of objects for the fledglings to play with, hereafter referred to as toys. Some (permanent) toys were available for the whole experiment and others were alternated on a daily basis (alternative toys). The experimental design consisted of two treatments A and B. Individuals in treatment A (pens 1-2-3) were offered mouse mimics as permanent toys, while individuals in treatment B (pens 4-5-6) were offered bottle corks. As alternative toys in both treatments we provided two types (cones versus twigs) and two sizes (large versus small), that is, large pine cones (Austrian pine, *Pinus nigra*) versus small pine cones (Scots pine, *P. sylvestris*), and large (6 cm) versus small (3 cm) twigs. At any

given time there was one permanent and one alternative toy per bird in each pen (e.g. four mouse mimics plus four long twigs in pens 1-2-3, and four bottle corks plus four long twigs in pens 4-5-6. The mouse mimics, made of grey fur with the size and proportions of wild adult mice, were acquired in a pet shop where they were sold as toys for cats.

We monitored the behaviour of the experimental birds daily between 20 July and 9 August, with the exception of 30 and 31 July. There were two daily observation sessions lasting 75–90 min each, one in the early morning (0630–0830 hours) and one in the evening (1700–1900 hours). Alternative toys were changed every day before the observation sessions started. There were four to five sessions per alternative toy. Observation times per alternative toy were as follows: large cone, 660 min; small cone, 720 min; long twig, 840 min; short twig, 660 min. Kestrels were fed whole day-old cockerels, *Gallus gallus domesticus*, ad libitum once a day at the end of the morning observation period. Food remains were removed daily. Birds had had the same feeding time and diet before being transferred to the test pens.

The observer (J.M.) walked continuously along the six pens during the observations looking through the one-way mirrors, and stopped only to record instances of object play. This procedure precluded the calculation of absolute frequency of play instances, but permitted us to record more play instances than if we had observed pens individually for the same amount of time.

We recorded as play all manipulations of objects by the kestrels, including experimental toys as well as wood chips and fallen kestrel feathers. For each observation we recorded: (1) time, (2) the individual playing, (3) object type, (4) brief description of the action.

Most observations of object play in raptors in the literature involve juveniles (Fagen 1981; Palmer 1988; but see Bildstein 1980). To determine whether the relative frequency of object manipulation was related to age, we introduced a pair of adult kestrels into each of the six test pens. These six pairs had just finished breeding in the outdoor pens. We observed them between 13 and 22 August 1994, although the birds had been in the test pens since 10 August to adjust to their new surroundings. Observation time amounted to 6 h (1 h per day during 6 days).

The adult birds were divided into two treatments, and two samples of each toy previously offered to the juveniles were placed in the pens simultaneously. The three pairs in pens 1-2-3 were offered two mouse mimics, two large cones, two small cones, two large twigs and two small twigs. Pairs in pens 4-5-6 were offered two bottle corks and the same alternative objects as in treatment A. Objects were placed in two lines along the floor of the pens, so we could deduce if any had been moved. The birds were fed day-old cockerels ad libitum once a day.

Statistical Analyses

We used generalized linear models (GLM) (Nelder & Wedderburn 1972; Dobson 1983; McCullagh & Nelder 1983) fitted with the program GLIM (Baker 1987) to analyse the results. Generalized linear models are a class of models from which linear regression, ANOVA and ANCOVA are particular cases. GLM permit a wider range of relationships between the response and the explanatory variables and the use of other error formulations when the normal error is not applicable. A GLM is defined by three components: a linear predictor (defined as the sum of the effects of the explanatory variables), an error function (that depends on the nature of the data) and a link function (that establishes the relation between the response variable and the linear predictor). More details on the applicability and use of GLM can be found in Crawley (1993).

As the number of play instances with the toys were counts, we assumed that the errors followed a Poisson distribution and we used logarithms as the link function (Crawley 1993). The proportion of play instances directed to the permanent toy was modelled as a binomial distribution with a logit link, the binomial denominator for each individual being the total number of instances it played with experimental toys. For each variable we fitted full models considering the factors: treatment, pen (nested within treatment), sex and the interaction of sex with treatment. The significance of each factor and interaction was assessed by step-wise backwards elimination from the full model. The increase in deviance of the model when a factor or an interaction was removed was checked against the distribution of a chi-square with the same degrees of freedom (*df*) as the increase in *df* of the model. Factors or interactions

Table I. Analysis of deviance for the variable 'number of play instances with the experimental toys'

Source	Reduction in deviance	Reduction in <i>df</i>	<i>P</i>
Treatment	0.518	1	NS
Pen within treatment	75.180	4	<0.0001
Sex	2.736	1	NS
Sex*Treatment	0.556	1	NS

Full model: deviance=21.36, *df*=15. Significance of each factor and interaction was assessed by backwards elimination from the full model.

with a $P > 0.05$ were considered not significant. We removed non-significant factors until all remaining factors were significant and a minimum adequate model was obtained. When the ratio deviance:*df* of the initial minimum adequate model suggested overdispersion in the data (Crawley 1993), the deviance of the model was scaled (i.e. the scale parameter being estimated from Pearson's chi-square, Aitkin et al. 1989) and the significance of the final model rechecked. This is the same as assuming that the variance of the error is equal to the mean times the scale parameter.

To test whether the kestrels selected a size (large or small) or type (cone or twig) of alternative toy, and whether this selection could be related to the treatment, sex, pen or individual, we fitted GLM models to a contingency table defined by the factors treatment, pen (nested within treatment), sex, individual (nested within the interaction of sex with treatment), toy size and toy type. The predicted variable was modelled as a binomial variable using as denominator for each individual the total number of instances it played with the alternative toys. A logit link was used. Initially, a full model with all possible interactions was fitted. The significance of interactions, starting with those of higher order, and then of single factors, was assessed by backwards elimination until a minimum adequate model was obtained.

To test for a temporal correlation in play behaviour among fledglings housed in the same pen we fitted a GLM model to the total number of play instances with objects of each individual each day of observation, using a Poisson error and a log link. Initially, a model with the factors pen, sex, day and interaction between pen and day was fitted. The significance of the interaction was tested by backwards elimination from the full model.

RESULTS

We observed the fledglings interacting with inanimate objects 506 times. We considered all these interactions as object play. The most frequent form of object manipulation was 'pecking' (40.8% of all instances), followed by 'grabbing object with talons and pecking at it' (19.7%) and 'jumping and flying while holding object' (14.5%). Other types of interactions and their relative frequency were the following: 'object pounced upon' (7.2%), 'grabbing object with talons' (6.2%), 'striking and kicking object with talons' (5.8%), 'hopping around in wood chips' (2.1%), 'pulling object' (1.6%), 'lay down upon' (0.83%), 'rolling object with beak and talons' (0.5%) and 'balancing upon object' (0.33%).

The adult kestrels in the experiment were never seen manipulating objects during the observation sessions. Moreover, these same objects remained in the same positions as at the beginning of the experiment, and therefore we can conclude that the adults never manipulated them during the 6 days of the experiment.

Fledglings in both experimental treatments played a similar number of times with the experimental toys (Table I, Fig. 1). There were no significant differences associated with sex or with the interaction of sex with treatment, but there were significant differences associated with the pen. Individuals in certain pens played significantly more with the experimental toys than individuals from other pens.

There were significant differences associated with treatment in the proportion of play instances directed to the permanent toy (Table II). Fledgling kestrels with mouse mimics as permanent toys directed a greater proportion of play instances to them (treatment A: $\bar{X} \pm \text{SD} = 0.75 \pm 0.15$) than

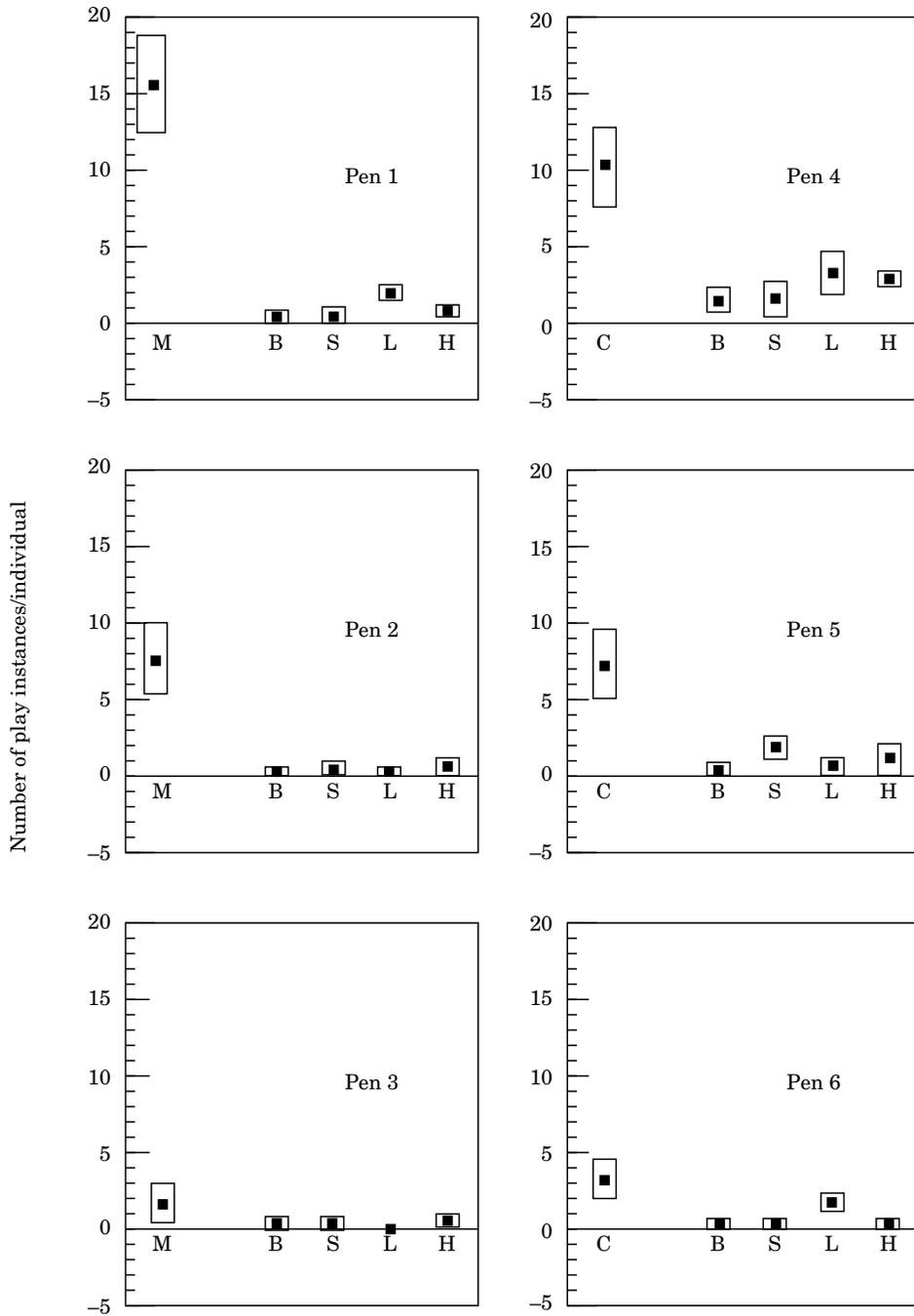


Figure 1. Mean number of play instances per individual (■) with the experimental objects in each of the six test pens. Bars indicate the standard error of the mean. Objects offered permanently: M, mouse mimic; C, bottle cork. Objects offered alternatively: B, big cone; S, small cone; L, long twig; H, short twig.

Table II. Analysis of deviance for the variable 'proportion of play instances with the permanent toy'

Source	Increase in scaled deviance	Increase in <i>df</i>	<i>F</i>	<i>P</i>
Treatment	12.48	1	11.98	0.0035
Pen within Treatment	1.84	4	0.44	NS
Sex	0.88	1	0.85	NS
Sex*Treatment	0.06	1	0.06	NS
Error	15.63	15		

Scale parameter=1.55. Full model: deviance=24.23, *df*=15. Significance of each factor and interaction was assessed by backwards elimination from the full model. Significance was assessed after scaling because of significant overdispersion.

fledglings with bottle corks as permanent toys (treatment B: 0.52 ± 0.22). There were no differences associated with sex, pen or the interaction of sex with treatment.

Considering play instances with alternative toys (Table III), the only significant main effect was toy type. Kestrels preferred twigs to cones (57 versus 34 play instances, respectively). There were significant interactions between pen and toy size and highly significant interactions between individual and toy size, and individual and toy type. This indicates that there were individual preferences among the fledglings in relation to the alternative toys, and that these preferences were to some extent dependent on the pen where the birds were housed, but independent of fledgling sex or experimental treatment.

The number of play instances with objects for each individual each day showed a significant interaction between pen and day (change in deviance=210.4, change in *df*=100, $P < 0.0001$).

Individuals housed in the same pen thus tended to play more on the same days.

DISCUSSION

The results of the experiment agree with our initial predictions, based on the ideas of Sherrod (1983), that raptors devote a certain amount of time and energy to manipulation of objects during the post-fledging period. These will be directed to prey, or objects resembling prey, if they are available but to other objects if not. In our experiment, fledglings that had mouse mimics as permanent toys did not play more often than those that had bottle corks, but they did prefer mouse mimics to the alternative objects. On the other hand, fledglings that had bottle corks as permanent toys did not prefer them to the alternative toys. It seems, therefore, that the type of objects available does not necessarily affect the intensity of play, but if

Table III. Analysis of deviance for play instances with alternative toys considering the factors treatment (T), sex (S), pen (P) nested within treatment (T*P), individual (I) nested within the interaction of treatment, pen and sex (T*P*S*I), toy size (Size) and toy type (Type)

Source	Increase in deviance	Increase in <i>df</i>	<i>P</i>
T*P*S*I*Size	35.46	11	<0.001
T*P*S*I*Type	32.93	11	<0.001
T*P*Size	13.85	4	<0.01
Type	8.10	1	<0.005

Full model: deviance=14.93, *df*=15. The asterisks between factor acronyms denote interactions. The significance of each source of variations was assessed by step-wise backwards elimination from the full model starting with higher order interactions. Only significant factors or interactions are given.

possible raptors will choose to play with objects resembling their usual prey. Bildstein (1980) observed that northern harriers, *Circus cyaneus*, chose to play with corn cobs of a size similar to their habitual prey. Also, redbreasted sparrowhawks, *Accipiter rufiventris*, showed more interest in pine cones covered with crow feathers than in bare cones (Simmons 1984).

Our results also suggest that social facilitation may affect object play in American kestrels. Kestrels housed in the same pen tended to play with a similar intensity, preferred the same alternative objects, and played more often on the same days. All these observations suggest that fledglings may be encouraged to play when they watch other individuals playing. Free-ranging American kestrel fledglings tend to join other fledglings during the post-fledging period (Lett & Bird 1987), a behavioural trait also observed in related species, such as the European kestrel, *Falco tinnunculus* (Bustamante 1994). Varland et al. (1991) observed social facilitation during social hunting in free-ranging American kestrels during the post-fledging period, although they did not find evidence that group size affected the rate of acquisition of hunting skills (Varland & Loughin 1992). On the other hand, Edwards (1989) reported copying behaviour during the maturation of fishing skills within broods of ospreys, *Pandion haliaetus*, in the post-fledging period, and that fledglings in broods of two progressed faster than singletons.

Play with objects has been observed, although infrequently, in adult raptors (e.g. Bildstein 1980), but our adult American kestrels housed in similar conditions to fledglings showed no interest in playing with the same set of objects. This observation suggests that manipulative play with objects is more important at the time when maturation of hunting behaviour takes place than at later stages in the life of raptors. Thus, it provides some support to the hypothesis (Fagen 1981; Bekoff & Byers 1985) that object play has a function in the maturation of hunting skills of the young of predatory species.

The lack of play activity in adults could also be related to prey recognition. Young birds would play with objects to investigate whether they are edible. Adult birds, on the other hand, would have no need to investigate as they already have the experience that those objects are not prey. This hypothesis, however, does not seem to

explain why the majority of young birds do not play.

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