4-1984

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Recommended Citation
Bekoff, M. (1984). Social play behavior. Bioscience, 34(4), 228-233.

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ABSTRACT

Recent studies clearly indicate that animal play is an important behavioral phenotype, and that detailed analyses of the phenomenon are useful for furthering our understanding of the evolution of social behavior and the interaction of phylogeny, ecology, and behavioral development. This article is concerned mainly with evolutionary, ecological, and developmental aspects of social play behavior in mammals.

For many years, studies of animal social play behavior produced mainly vague descriptions of a phenomenon that everyone saw, but few took seriously. As Byers (1981, p. 1493) noted:

> Study of animal play historically has languished at the fringes of behavior research. Suspicions that play did not really exist or that it was a trivial phenomenon kept many investigators away. However, like an unwelcome guest, play continued to present itself to field workers.

Early observations of play usually were accompanied by grandiose, eponymous (for example, the Schiller-Spencer Surplus Energy Theory) theories (how could anyone refute something to which he attached his name?), explaining everything, and in some cases, nothing (Bekoff 1976a). Perhaps if it was as much fun to study play as it is to engage in it, more would be known about the activity.

Although it has been a long time in coming, recent reviews of social play behavior (M. Bekoff 1978, Bekoff and Byers 1981, Fagen 1981, Smith 1982 and accompanying peer commentaries, Symons 1978a,b) clearly show that the study of play is finally becoming a welcome guest. One of the main reasons behind the increased vigor and rigor with which play research is being conducted stems from broad multidisciplinary interest in the activity by neurobiologists, population biologists, demographers, exercise physiologists, pharmacologists, ecologists, and evolutionary biologists (Beatty et al. 1982, Bekoff and Byers 1981, Bekoff et al. 1980, Fagen 1977, 1978, 1981, Martin 1982, Meaney et al. 1981, Panksepp 1979, Welker 1971). Scientists who otherwise wrote play off as a topic not worthy of serious study came to realize that detailed analyses of play could further our understanding of the evolution of social behavior and social organization, the interface between phylogeny and ontogenetic processes (neural and behavioral), and learning. Indeed, Wilson (1977) lists play as one of five major areas of sociobiology warranting detailed explanation (the others are kin selection, parent-offspring conflict, the economic role of territory, and homosexuality; play certainly keeps good company!).

WHAT IS PLAY?

Play is a vague word that is used to describe a wide variety of motor patterns. Although most people have little trouble recognizing play, it has been difficult to develop a general, comprehensive definition (see Fagen 1981, Appendix I, for a list of definitions). As more and diverse species are studied, the definitional

problems may become increasingly difficult, but a definition also may be more necessary. The possibility remains that "play" may be broken down into finer categories that can be more easily characterized.

Definitions of play based on structure (what individuals do when they play) are problematic, because play assumes many different forms in different mammalian orders. General definitions based on function, are, at this time, impossible to develop, because the function(s) of play largely remain a mystery. The enormity of the problem of definition is evidenced by the fact that the word "play" itself often is used in definitions of play.

Some defining characteristics of play include: activities from a variety of contexts are linked together sequentially; specific sets of signals (visual, vocal, chemical, tactile) including gestures, postures, facial expressions, gaits, odors, and sounds are important in the initiation of play; certain behaviors such as threat and submission, are absent, or occur infrequently; there are breakdowns in dominance relationships, role reversals, changes in chase-flee relationships and contact time, and individuals engage in self-handicapping; and there are detectable changes in individual motor acts and differences in sequencing when compared to nonplay situations (see Bekoff and Byers 1981, Table 11.1 for references, and also Chalmers 1980a, Fagen 1981). Not all of the characteristics apply to all species, nor is it presently possible to say that at least two or three must apply in order for the activity to be called play.

Regardless of what definition is offered in different studies, a common component is that virtually all postnatal activities (performed in nondeprived settings) that appear functionless are usually referred to as play. Furthermore, striking similarities between prenatal activity (motility; A. Bekoff 1978, Hamburger 1963, Oppenheim 1974) and postnatal play become apparent. As Chalmers (1980b) and Thelen (1981) pointed out, diverse behaviors may have common ontogenetic (and phylogenetic) precursors.

Prenatal Motility

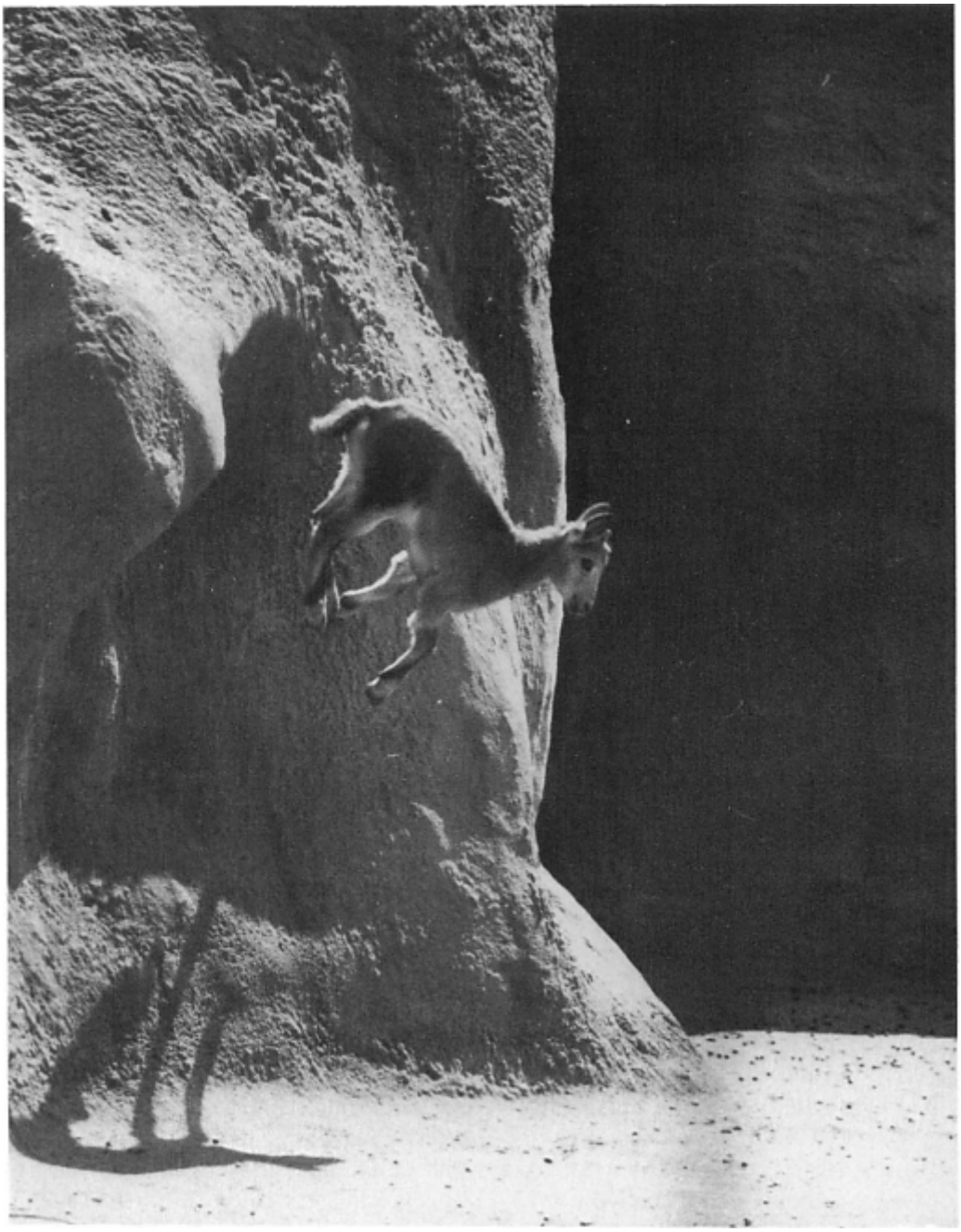
One of the more interesting findings in this field of research that is most relevant to the present discussion is that although overt motility at different stages of chick embryonic development does not resemble later perinatal or postnatal behaviors such as hatching or walking, there is a strong resemblance in the covert patterns of muscle activation and coordination between early and later motility and between hatching and walking, as demonstrated by electromyographic (EMG) recordings (A. Bekoff 1978). These findings do not necessarily mean that motility and later behaviors are functionally isomorphic, nor do they attend to the important issue of whether the later (ontogenetically) behavior patterns are really the same as ones that appeared earlier in development (Bateson 1978). Rather, the discovery that the underlying neuromuscular patterning of both prenatal and postnatal behaviors may be the same, coupled with experimental documentation that prenatal movements are spontaneous or endogenous, provides us with a new perspective from which we can view postnatal play behavior.

Postnatal Play

The perspective provided by considering prenatal development is that outwardly purposeless motor activity is a regular feature of vertebrate ontogeny that seems to have reached the peak of its expression in mammals, in which it is continued, long after birth, as play (Bekoff and Byers 1981). It seems as if early activation of the developing neuromuscular system was selected for at some point in vertebrate evolution. This requirement for activity became more pronounced, elaborate, and longer-lived (ontogenetically) as the vertebrate neuromotor system became more complex.

Because prenatal life is basically nonsocial and opportunities for motor activity are limited, likely benefits of prenatal activity include the facilitation of neuromuscular development. Therefore, this was probably the phylogenetically oldest function of postnatal outwardly purposeless motor behavior (play).

Figure 1. Play by young (and old) animals may involve frantic and rapid locomotor activity and also may be risky. Here, a Siberian ibex kid about 8-10 weeks of age banks off a vertical wall in the middle of a play bout.



Photograph by John A. Byers.

At this point, natural selection probably began to mold this postnatal behavior in response to a number of selection pressures that were most likely consequences of a species' adaptive syndrome (Eisenberg 1981) (e.g., its size, habitat, and food habits) and its degree of adult neuromuscular and behavioral complexity. The result, as we observe it today, is play. As more descriptions of play in different

mammalian orders become available, we should be able to fill out a phylogenetic tree of play and thus may be able to deduce its evolutionary history more precisely.

Therefore, there are two possible avenues of continuity between prenatal and postnatal motor activities. The first is phylogenetic, in that embryonic motility may be ancestral in evolution to postnatal play. Many vertebrates that show prenatal motility typically do not play (e.g., fish, amphibians, reptiles, many birds, and perhaps a large number of mammals). The second is ontogenetic, in that there may be developmental continuity between prenatal motility and postnatal play.

A Working Definition of Play

Similarities between prenatal motility and postnatal play are obvious: both appear to be functionless, and in many cases, play, like motility, appears to be spontaneous. One characteristic of locomotor play is that of sudden, persistent, frantic motor activity (e.g., locomotor-rotational movements; Wilson and Kleiman 1974) that may include undirected flight.

Having clarified these points, play will be defined as it is seen in natural conditions or in settings that closely simulate them. *Play is all motor activity performed postnatally that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and altered temporal sequencing* (Bekoff and Byers 1981, p. 300). (Whether an activity is deemed to be "purposeless" may depend on the inventiveness of the observer.[1]) If the activity is directed toward another living individual, it is called social play; if it is directed toward an inanimate object(s), it is called object play; if the activity carries the individual in a seemingly frantic flight about its environment, it is called locomotor play (Figure 1). Both social and object play can be locomotory in nature, and what has been referred to as self-play could include object and locomotor play. In some cases, play may be "involuntary." Many of the first interactions of young mammals, either with littermates, parents, or objects, seem to develop almost reflexively from fidgeting and mouthing. For example, early rooting and mouthing movements used in nursing, when transferred to the leg or face of a littermate, are usually called play. Are these early behaviors simply the result of endogenous neural activity? Are the movements nonspecific reflexes that are channeled by whatever is available (e.g., nipple or limb)? Why do individuals engage in self-play?

The emergence of vigorous play from more subtle forms of interaction suggests that the phenotype of play that is observed at a given moment depends on the motor and sensory abilities of the developing individual. And, just because the earliest vestiges of play may be involuntary, this does not mean that with increasing experience (social and otherwise), play is not modifiable. Of course it is. As Bateson (1976) suggested, developmental control mechanisms may themselves be modifiable by the environment in which an organism grows up.

To summarize, the apparent lack of purpose of play activity, its spontaneity, and its emergence from early fidgeting movements suggests that there may be some continuity between prenatal motility and postnatal play. Whether the two activities simply look discontinuous because of the differences between prenatal and postnatal environments is open to speculation. The outward purposelessness of both suggests that there has been selection for early rehearsal of certain motor activities. Although the apparent lack of purpose of play is an important defining characteristic, it really is not functionless at all.

ECOLOGY OF PLAY BEHAVIOR

Habitat type, resource availability, and the social environment can affect the performance (type and amount) of play activities (Baldwin and Baldwin 1973, 1976, Berger 1979, Fagen 1981, Nowicki and Armitage 1979, Sussman 1977, Symons 1978a, Wilson 1973). Field studies of the same species living in different habitats provide useful information concerning the relationship between proximate environmental

conditions and the development of play. For example, Berger (1979, 1980) found that social development differed in natural populations of bighorn sheep *(Ovis canadensis)* living in different habitats. Desert sheep living in the Santa Rosa Mountains of southern California where the presence of Cholla cactus *(Opuntia* spp.) made play risky, played significantly less than sheep living in the Chilcotin area of British Columbia, Canada, where there were more suitable play areas such as grassy fields and sand bowls. The structure of play also differed; desert yearlings never were observed to engage in rapid locomotor play, undoubtedly because of the risk of running into cacti. Berger also found that sheep in British Columbia lived in larger groups and grew up in a more diverse social environment. They had more playmates and showed greater diversity in play patterns.

The necessity for studying allopatric conspecifics is clearly exemplified in this study. Speaking about *the* structure and function of play in *the* bighorn sheep would be misleading because of the influence of habitat and the social environment on the development and elaboration of play activities.

EVOLUTION, LIFE-HISTORY PATTERNS, AND PLAY

> Social play reflects biological adaptation. Like other aspects of social behavior, it has been selected to adjust to a broad range of environmental conditions in the service of inclusive fitness (Fagen 1981, p. 387).

Evolutionary considerations of play are becoming more numerous, and this perspective has helped to clarify various aspects concerning the development of the activity, its structure, how the nature of play may vary with particular play partners, and its functions (M. Bekoff 1978, Bekoff and Byers 1981, Fagen 1977, 1978, 1981, Symons 1978a,b). The application of various evolutionary models to play behavior (such as viewing play as an Evolutionarily Stable Strategy, ESS; Maynard Smith and Price 1973) provides interesting suggestions concerning what animals should do in this or that situation if they behave as hawks, doves, cheaters, etc. But, overzealous interpretation of theoretical results must be tempered by a more generic approach to play, in which the activity is quantitatively analyzed and testable hypotheses are entertained. Facile evolutionary explanations of play (Byers 1981) or other behavioral patterns tend to imply that a lot more is known about the activity than actually is known. Furthermore, as discussed above, one of the most exciting aspects of developmental research involves the dissection and reconstruction of how behavior unfolds throughout life. Using inclusive fitness as the ultimate (in both senses of the word) reason to explain why animals play tends to remove attention from the fact that selection operates at all stages of development (Williams 1966) and that individuals need to successfully meet challenges at all ages in order to survive to the next stage (Galef 1981). Evolutionary and developmental studies should complement one another; they are not mutually exclusive.

Play appears to have evolved mainly in K-selected species (Fagen 1981), especially mammals, in which there is a prolonged period of immaturity, dependence on adult care-giving, and a high encephalization quotient (EQ = ratio between the observed brain weight and the expected brain weight for a defined body weight; Eisenberg 1981, Jerison 1973). However, it must be remembered that only very few species actually have been studied.

In species in which play has been observed, young individuals typically play more than adults; there appears to have been strong selection for the appearance of play early in life (and its relative absence in later life) (Fagen 1977). Even if food is limited, due perhaps to early weaning (naturally or experimentally induced), young individuals may show a facultative response to decreased food and pack the experience into a shorter period of time (Bateson and Young 1981, see also Bateson et al. 1981). Therefore, the total amount of play may be the same for individuals growing up in conditions in which resource availability differs, but the way in which play is temporally distributed (with age) might vary.

It also has been suggested that the benefits derived from play may decrease with age (Caro 1981, Chalmers and Locke-Hayden 1981). But, it is necessary also to ask whether the benefits derived from play decrease because animals spend less time playing, or whether animals spend less time playing because they do not get as much out of it. As individuals get older and more independent, there are more things that they need to do of their own accord, and constraints of competing activities may also affect the observed developmental time-course for play (Fagen 1981, Fossey 1979, Sharatchandra and Gadgil 1980, Wilson 1982). As Fagen (1981) noted, animals have limited time and energy to devote to survival, growth, and reproduction, the important components of life-histories. Obviously, the amount of time devoted to a specific activity depends on how much goes to others.

WHY PLAY? FUNCTIONAL CONSIDERATIONS

Study of the function of play is a study of the process through which natural selection shaped this behavioral phenotype. Therefore, it is different from the study of proximate causation, which seeks to define the immediate stimuli and physiological mechanisms that control play. It also needs to be stressed that not all of the beneficial consequences of a behavioral pattern constitute its function (Hinde 1975, Symons 1978b, Williams 1966). By function, I mean the specific consequences of a behavioral pattern that have resulted in its fixation in a species' repertoire by natural selection (Bekoff and Byers 1981, p. 312). The possible functions of play must be studied with respect to both the young individuals that are playing at a given age (immediate benefits) and to the delayed, cumulative consequences possibly affecting fitness.

At this juncture there is no use belaboring an obvious point: ideas about the functions of play (reviewed in Bekoff and Byers 1981, Fagen 1981, Smith 1982, Symons 1978a,b) must be taken as what they are -- suggestions. Although it may be all right to favor one hypothesis over others, it would seem unwise to discount a reasonable suggestion as being inapplicable, given the enormous variability of play (even among conspecifics). Most authors conclude that there is no one function of play. Data from wholesale deprivation studies (Bekoff 1976a,b, DeGhett 1977) have provided little insight into the question of why animals play.

In his consideration of the beneficial aspects of play, Fagen (1981, p. 271) lists six overlapping hypotheses: play develops physical strength, endurance, and skill; play regulates developmental rates; play experience yields specific information; play develops cognitive skills necessary for behavioral adaptability, flexibility, inventiveness, or versatility; play is a set of damaging behavioral tactics used in intraspecific competition; and play establishes or strengthens social bonds in a dyad or social cohesion in a group. Bekoff and Byers (1981) idealize the possible functions as involving motor training, socialization, and cognitive training. Here I will consider only the motor training and social cohesion hypotheses.

MOTOR TRAINING

Play appears to be important in the development of strength, endurance, and various skills. Different motor patterns from various contexts are used in play, and repetition of these motor patterns along with vigorous exercise may be important in both the development of general physical fitness and in the development of particular skills. Smith (1982) concluded that play primarily affords practice for certain socially competitive skills (especially agonistic and predatory; see also Symons 1978a), and that the development of social skills that also appear to be associated with play experience are actually only incidental benefits. But, Smith admits that at present, evidence is not available to support this notion.

Structural analyses of play support the training hypothesis (Biben 1982, Byers 1977, 1980), but Fagen (1981) believes that they do not explain adult play, courtship play, and social play. However, if skill

development is considered to be important throughout life, then it would be entirely possible that an otherwise experienced adult could be inexperienced when it comes to the skills needed in courtship and mating.

Fine-tuning

Associated with the training hypothesis and the common observation that play borrows actions from various contexts (except, perhaps, those behaviors used in the communication of play intention; Bekoff and Byers 1981 and references therein) is the notion that while playing, an individual may be looking for an optimal goodness-of-fit of individual behavioral patterns in situations in which they do not have to pay severe consequences for mistakes (Klopfer 1970); they experiment with different combinations of various behaviors that would never be tried .under pressure (Bruner 1974). Animals may also be learning to make fine motor movements from more global actions involving many muscles and body parts; play may be part of a calibration program (Gould 1982).

Fine-tuning provides behavioral flexibility, useful when conditions (social and otherwise) change. The ability to match behavioral responses with changing situations may be a skill that is necessary throughout life; it could facilitate the social integration of individuals into a group under different environmental conditions (Nowicki and Armitage 1979) and increase success in catching different prey.

Support for the "fine-tuning-through-repetition-and-training" hypothesis comes from a wide variety of studies (Baerends-van Roon and Baerends 1979, Berger 1980, Bruner 1974, Chalmers 1980b, Latour 1981, Mason 1979, Nowicki and Armitage 1979, Pellis 1981; but see Symons 1978b). In many species there appears to be strong selection against the continued addition of new motor patterns whenever something new is confronted. Thus, fine-tuning could evolve as an adaptive skill via selection for the ability to slightly modify existing motor patterns and the way in which they are linked sequentially in order to deal with changing situations. Here, the major question is whether the ability to fine-tune responses to proximate conditions conferred a selective advantage that led to the evolution of play in animals (Bekoff and Byers 1981).

SOCIAL COHESION

The social cohesion hypothesis suggests that play may be a mechanism through which social attachments are formed and social bonds strengthened and maintained (M. Bekoff 1977, Rappold 1976, Latour 1981, Panksepp 1981, Wilson 1973). (Of course, social bonds also may be formed through activities other than play, including mere exposure, but here I consider only play behavior.) In some species in which play occurs in high frequencies among young individuals, there may be a cumulative effect that might reduce and delay the tendency to disperse (Bekoff 1977, Rappold 1976). Delayed dispersal may be associated with the existence of cohesive social groups in which different-aged individuals live (Armitage 1981, M. Bekoff 1977, Bekoff et al. 1981).

Smith (1982) is critical of the cohesion hypothesis. He wrote that if play is important in social bonding "it would be expected to occur most in species with social groups of moderate size, and not in solitary species" (p. 145). The reason for this assumption is not clear. Theories relating play to social bonding and dispersal attempt to account for both intra- and interspecific differences in the developmental time course of play (and other behaviors). They stress that *differential* play experience (differences in the quality, amount, and/or distribution of play among group members) may affect the *probability distribution* of individuals leaving their natal group. Smith's (1982) statement "if social play serves a bonding function it would not be expected to occur if offspring leave their natal group to join another after the juvenile period"

(p. 145) ignores the differential effects that play may have on individuals growing up in the same group. The question is not whether they play, but how much.

Fagen (1981) is critical of the cohesion hypothesis mainly because he can find exceptions to the "rule." But he recognizes the cohesion hypothesis as one of three that deserves consideration in evolutionary analyses of play. "Without a doubt, each hypothesis will prove valid in particular instances" (Fagen 1981, p. 358).

Social Cohesion and Fine-tuning

A combination of these two hypotheses may be important in both understanding the act of dispersal and how dispersing individuals respond to new environmental conditions. Geist (1978) suggested that play facilitated development of flexibility and prepared an individual to be a successful disperser, or colonizer. The dispersal phenotype would be characterized by an adaptable animal capable of tolerating diversity (Fagen 1981).

Fagen (1981) stated that the flexibility hypothesis and the social cohesion hypothesis made opposing predictions about dispersal. I believe that both may work hand-in-hand. As mentioned above, the cohesion hypothesis does not state that some individuals play and others do not. It suggests that differential early play (and other) experience may predispose some individuals to remain in their natal area and others to leave. With few exceptions, all individuals probably partake in some play early in life (although the age distribution may vary according to food resources [Bateson and Young 1981] or dominance rank), and therefore, all individuals would be primed to varying degrees to be able to deal with novel problems both within, and outside of, their natal home range. The question that needs to be answered now is how much (little) play is necessary to produce an individual who can fine-tune responses to various external conditions and if this amount of play is insufficient for the formation of social bonds strong enough to delay dispersal. That is, if play is important in the formation of social bonds, and if individuals who have not played enough to form bonds leave their natal group, have they still had enough play experience to be able to deal with the novel situations to which they may be exposed during dispersal? I agree with Geist's suggestion about the preparatory role that play may serve for dispersal, and I think that it is compatible with suggestions relating differential development play to dispersal.

All theories of play must be given their day in court. Supportive and contrary evidence always will be forthcoming. Future research is filled with exciting possibilities, such as: Why do different functions apply to different species? Which functions may be widespread phylogenetically? Do (and why do) different functions apply to conspecifics living in different habitats? Basic information concerning partner preferences, play-signals, self-handicapping or restraint, and the way in which "rules" of play develop are needed for most species, including those in which play has been studied. Data that tie together evolution, ecology, and development are required. Play, that unwelcome guest, is here to stay.

NOTE

[1] Gail Michener, University of Lethbridge, Lethbridge, Alberta, Canada, personal communication, December 1980.

ACKNOWLEDGMENTS

This manuscript was initially prepared while I was supported by a John Simon Guggenheim Memorial Foundation Fellowship. I thank Thomas Daniels, Joel Berger, and John Byers for discussing many of the

topics that are considered in this paper. Jeanie Cavanagh and Mary Marcotte typed the manuscript. Two unidentified referees provided useful suggestions, and I am grateful to them.

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