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Title: PLAY BEHAVIOR IN THE GOLDEN HAMSTER

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Dennis L. McDonald

Intensive observations were made of play behavior in the young hamster (Mesocricetus auratus) from 14 to 54 days of age. Behavior was recorded using movie film and a multi-channel event recorder.

Play was first seen at 14 days of age. The amount of play increased rapidly thereafter, remaining relatively high until about day 40. Playing then decreased, becoming sporadic by day 54. This decline corresponded to an increase in agonistic encounters.

Play bouts were generally shorter during the first days of play, and also shorter after day 40, as aggression increased. When play bout duration was plotted as a survivorship function, the result was significantly different from a straight line, indicating that the probability of a bout ending is not independent of how long it has lasted.

Play bouts were relatively simple at first, becoming more complex as motor patterns were added during ontogeny. The sequence of motor patterns in playful interactions resembled the patterns later seen in agonistic encounters.

The data are discussed with regard to some of the current theories of play. Play does not seem to function for exercise or the formation of positive social bonds. It is hypothesized that play in this species may be only the ontogeny of agonistic behavior.

PLAY BEHAVIOR IN THE GOLDEN HAMSTER

by

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PLAY BEHAVIOR IN THE GOLDEN HAMSTER

INTRODUCTION

Most people have, from their own experiences, an extensive and personal knowledge of human play. They can also generally agree between themselves as to whether a member of another animal species is, or is not, playing. Play in these other species has nevertheless remained a "problem" category of behavior; controversial with regard to its function, and difficult to define.

Most major types of behavior -- for example, those associated with aggressive, sexual, or predatory activities -- are fruitfully discussed in terms of their purpose; their contribution towards an organism's survival and the passing of his genes to the next generation. Thus the field of behavioral biology can be brought under the aegis of the theory of natural selection. The purpose of play behavior, however, is not easily understood. Loizos (1966) states that a typical attitude towards animal play is to consider it useless, making play a category of behavior which is by definition of no survival value to the organism.

The idea that play is unimportant in terms of natural selection is implied in the "surplus-energy" theory of play. The basic idea of this theory (which Groos (1898) attributed to the poet Schiller and Herbert Spencer) is that an animal plays when he has completed all necessary activities, but still has energy left which must be expended. Even among authors who consider play of some ultimate importance to the animal, a common characteristic cited of play behavior is its relative lack of seriousness (Marler, 1966; Müller-Schwarze, 1971) or lack of immediate purpose (Beach, 1945; Fagen, 1974; Eible-Eibesfeldt, 1975; Poole and Fish, 1975).

Perhaps as a result of play having no obvious function, some authors have decided that it is no longer a useful category of behavior (Schlosberg, 1947; Berlyne, 1969; Welker, 1971). Gilmore (1966) and Loizos (1966) have suggested that play has been used as a "wastebasket" category for behaviors that do not fit anywhere else.

Bekoff (1972, 1974b), however, has reaffirmed that play is a valid and useful category of behavior. In addition, several authors have stated that play -- whatever its function -- is of considerable importance to the developing animal (Groos, 1898; Dolhinow and Bishop, 1970; Hinde, 1974; Poole and Fish, 1975; Wilson, 1975). Loizos (1966) and Bekoff (1972) have argued that the importance of play is demonstrated by the large amount of time some species spend at it. Finally, Hinde (1974) states that although play is "impossible to define" it is nevertheless "inescapable in practice."

The Characteristics of Play

Although play is easily recognized, a precise definition of this behavior has proved elusive. As a result, play has most often been defined by listing its characteristics, or defined in a negative way, by listing what it is not. Some of the features commonly mentioned include:

1) Play only occurs when more basic needs (e.g., food, water, escape from predators) have been met (Welker, 1961; Loizos, 1966; Steiner, 1971; Poole and Fish, 1975).

2) Play is more typical of juvenile animals, since they often have the above needs fulfilled by adults (Beach, 1945; Loizos, 1966; Millar, 1968; Dolhinow and Bishop, 1970).

3) Play is not a "serious" activity in that it serves no immediate purpose (as above, also Wilson, 1975).

4) Play movements may be similar to those used in adult activities, but exaggerated, repeated, improperly oriented, or in disrupted sequence (Loizos, 1966, Marler, 1966; Poole and Fish, 1975). Fagen (1974) states that play has a highly variable structure whereas Müller-Schwarze (1971) emphasizes stereotyped behavior patterns in play.

5) Social play is often accompanied by signal patterns which indicate that a behavior is play. These signals have been called "metacommunication" (Loizos, 1966; Bekoff, 1972; Fedigan, 1972; Fagen, 1974).

6) The structure of play is relatively species specific (Groos, 1898; Beach, 1945; Müller-Schwarze, 1971; Poole and Fish, 1975; Wilson, 1975).

Play occurs in a variety of animals, especially mammals (Marler, 1966; Fagen, 1974; Eible-Eibesfeldt, 1975) and perhaps birds (Fagen, 1974; Eible-Eibesfeldt, 1975). Wilson (1975) has noted that the more intelligent and social species seem to play more. Other authors have singled out the primates and carnivores as playing the most, or having the most complex forms of play (Marler, 1966; Müller-Schwarze, 1971).

A list of some of the species in which play behavior has been studied, with selected references, is given in Table 1.

Theories of Play

The number of theories about play in the recent literature shows that it has not been dismissed as an invalid category of behavior. Some of the major theories, with references to supporters and critics, are summarized in Table 2. Among those listed, the theory that play aids in socialization seems to have the greatest amount of recent support.

Fagen (1974) has pointed out that there are really two major schools of thought regarding play; structuralism, which emphasizes the form and appearance of play, and functionalism, which concentrates on its causes and functions. Berlyne (1969) has also helped cut through the confusion of theories by stating, very sensibly, that a search to find one function for all types of play is probably hopeless. The diversity of activities which have been called play make it likely that more than one function is involved. In addition,

Table 1. Some of the species in which play has been studied, with selected references.

SPECIES	REFERENCE
Squirrel monkeys	Baldwin and Baldwin (1974)
Canids (wolves, coyotes, and dogs)	Bekoff (1974a, 1974b)
Chimpanzee	Bierens de Haan (1952)
Domestic cattle	Brownlee (1954)
Toggenberg goats	Chepko (1971)
Primates	Dolhinow and Bishop (1970)
Pony foals	Fagen and George (1976)
Steller sea lion	Farentinos (1971)
Vervet monkeys	Fedigan (1972)
Red squirrel	Ferron (1975)
Coyote	Fox and Clark (1971)
American black bear	Henry and Herrero (1974)
Ferrets	Lazar and Beckhorn (1974)
Rhesus monkeys	Meier and Devanney (1974)
California ground squirrels	McDonald (1977)
Polecats	Poole (1966)
Blacktailed deer	Müller-Schwarze (1968)
Laboratory rats and mice	Poole and Fish (1975)
Rhesus monkeys	Redican and Mitchell (1974)
Columbian ground squirrels	Steiner (1971)

Table 1 (Continued)

SPECIES	REFERENCE
Rhesus monkeys	Symons (1974)
Mongoose	Wemmer and Fleming (1974)
Domestic cat	West (1974)
Vole	Wilson (1973)

Table 2. Some theories of play, with selected supporting and critical references.*

THEORY	SUPPORTERS	CRITICS
Surplus energy	Schiller Spencer	Groos (1898) Beach (1945) Poole (1966)
Practice for adult activities	Groos (1898) Dolhinow and Bishop (1970 - primates)	Beach (1945) Loizos (1966) Poole (1966 - polecats)
Drive to play	Brownlee (1954 - cattle) Lorenz (1956) Chepko (1971 - goats) Poole (1966 - polecats) Eible-Eibesfeldt (1975)	Bekoff (1972) Müller-Schwarze (1968 - deer)
Familiarization with environment	Welker (1961) Bekoff (1972) Eible-Eibesfeldt (1975)	Loizos (1966)
Familiarization with conspecifics (socialization)	Dolhinow and Bishop (1970 - primates) Bekoff (1972) Gentry (1974 - Steller sea lion) Wemmer and Fleming (1974 - meerkats) West (1974 - domestic cats) S. Wilson and Kleiman (1974)	Poole and Fish (1975 - rats and mice) Baldwin and Baldwin (1974) Bekoff (1974b)
Exercise	Brownlee (1954 - cattle) Bekoff (1974a) Fagen and George (1974 - pony foals)	McDonald (1977 - ground squirrels)
Self-rewarding activity	Brownlee (1954 - cattle) Poole (1966 - polecats) Bekoff (1974a, 1974b)	Beach (1945) Loizos (1966)

*Note that when a specific animal is named with a reference, the author does not necessarily support (or reject) that theory of play on theoretical grounds, but has found (or failed to find) supporting evidence for it in work with that species.

a single form of play may have more than one function. Similar views have been expressed by Beach (1945), Loizos (1966), and Bekoff (1974b).

Rationale for Studying Play

There seems to be a recognized need for additional studies of play behavior. Marler (1966) felt that much more work needed to be done on play before we could even start to ask the right questions about it. Bekoff (1972), and Henry and Herrero (1974) have strongly recommended studies of the general characteristics of play be undertaken in as wide a range of species as possible.

To some extent, the number of different animals in which play has been investigated has increased recently. A 1974 symposium on play (published in the American Zoologist, Vol. 14) reported on studies of play in a wide variety of animals, including the domestic cat, ferrets, black bears, canids, and several primate species. But one problem with several of these studies, as with much of the previous work on play, was the generally small numbers of animals observed, and the relative lack of quantitative data. Statistical analysis of results was infrequent.

In addition, previous investigations had often ignored the ontogeny of play, treating this behavior as unchanged throughout the development of the animal. In 1945 Beach stated that studies of the ontogenetic development and regression of play in a single species would be valuable. Thirty-six years later Müller-Schwarze

(1971) said that such studies were rare; also Chepko (1971) stated that "More work needs to be done on the development of play behavior with age."

It is therefore valuable to investigate play in another species and to emphasize in the study (1) thorough observations and quantification of play and (2) any changes seen in play behavior during the period of its development in the young animal.

The Golden Hamster

The golden hamster (Mesocricetus auratus) was originally described by G. R. Waterhouse at a meeting of the Zoological Society of London in 1839. Little was known about the species, however, until 1930 when a colony of hamsters was established in Israel from a litter collected near Aleppo, Syria (Fulton, 1968). All the golden hamsters now in Europe and the United States are apparently derived from this one litter (Adler, 1948).

This species of hamster is found wild within an area extending from ". . . Rumania and Bulgaria southeastward through Asia Minor, the Caucasus, Israel, and the northwestern section of Iran" (Walker, 1968). They are burrowing animals, living on brushy slopes and steppes.

Few, if any, studies have been published dealing with the behavior or population dynamics of the golden hamster in the wild. Most of the work done with this species has centered around physiological or medical topics. A few studies (notably Dieterlen,

1959) have been concerned with a general description of the hamster's behavior in a laboratory situation. In addition, Eible-Eibesfeldt (1953) has written an extensive ethogram of the common hamster (Cricetus cricetus). This species is said (Rowell, 1961) to be almost identical in behavior to the golden hamster.

This animal was chosen to study for several reasons. First, there are no thorough investigations of the hamster's play behavior in the literature, although there have been brief descriptions of play within the general context of an ethogram, such as Dieterlen's. Rowell (1961) has also briefly described play in her study dealing with the formation and break-up of the hamster family group. In general, little work seems to have been done on play in rodents, though the studies of Wilson (1973; voles) and Poole and Fish (1975; laboratory rats and mice) are exceptions.

In addition, the hamster is readily and quickly bred in the laboratory. They do not require an excessive amount of space, allowing relatively large numbers of animals to be maintained and used for observations. The span of time in which they play (which was said to be from three to six weeks of age by Rowell (1961)) is short enough to be easily watched in its entirety.

Hamster play is not as complex as that of primates or carnivores, which may make it seem less interesting. Yet this lack of complexity may allow their play behavior to be more thoroughly understood.

In summary, play is at present a poorly understood category of behavior, despite the abundance of theories as to its function. Additional work in a wide variety of species seems needed before a clear picture of play can emerge.

The golden hamster was chosen as a suitable animal in which to study play. The primary purpose of the study was to investigate play behavior in the golden hamster, emphasizing (1) thorough observations and quantification of the data and (2) the changes which occur in play during its ontogeny. In addition, I sought to examine the applicability of some hypotheses about play's function in light of the data collected on this species.

METHODS AND MATERIALS

Maintenance and Handling of Animals

Adult hamsters were obtained from local pet stores and quarantined for five days before bringing them into the laboratory.

Males were used for breeding purposes only, and were housed in Bo-Kay fiberglass cages (60 x 15 x 15 cm). The females were housed in a large wooden cage, which was painted with a white, semi-gloss enamel. The cage was partitioned into five compartments (each 88 x 38 x 24 cm; floor area approximately 3344 cm^2), one for each female and her prospective litter.

Wire mesh covered the top of the cage and could be taken off to allow an unobstructed view for observations and filming. The cage floor was covered with hardwood bedding and contained cotton batting for nesting material. Pieces of balsa wood and a small piece of wire mesh (about 8 x 10 cm) tacked onto one wall were provided for the animals to chew on. Cages were cleaned every three to five days, except following the birth of a litter.

Water and Purina Rabbit Chow were given *ad libitum* to all animals. This diet was supplemented with rat chow, slices of apple, celery leaves, and a seed mixture ("8 in 1" Hamster Food or Otis Wild Bird Food) which contained milo, millet, cracked corn, and sunflower seeds.

The animals were kept under a 12 L:12 D photoperiod and the temperature maintained between 18° and 24°C.

The procedure used in mating the animals followed that recommended by Magalhaes (1968). Gestation is sixteen days. Except for briefly checking to see if a birth had occurred, a new litter was left undisturbed for at least one week. Disturbing the litter any earlier may upset a skittish mother, and cause her to kill the new pups (Magalhaes, 1968).

In the course of this study I obtained nine litters for observation. Four litters were born in October, 1976 and the remaining five in January, 1977. Four females had two litters apiece (one in October and a second in January); a fifth female had one litter in January. The litters will be referred to by the name of the mother and, when needed, a number; thus, Alice #1 (born October), Alice #2 (January), Victoria #1, Victoria #2, Helena #1, Helena #2, Charlotte #1, Charlotte #2, and Trixie.

Each litter used for observations consisted of seven pups, plus the mother. Litters of fewer than seven were not used, and if there were more than seven pups in a litter, I removed the extra animal at fourteen days of age. The pups were not sexed before beginning observations.

Formal observations began when a litter reached fourteen days of age, and continued until 54 days of age. The pups were not handled at all until day 30 because of the possibility that earlier handling can significantly influence speed of development (Daly, 1976).

On day 30, the mother and each pup were weighed and the pups marked so that individuals could be distinguished. Marks were made on the back and/or sides of a pup, using "Jamar D," a black dye.* Mother and pups were weighed again the day after observations ended. These weighings were done as a general check on the health of the animals.

After the end of observations on day 54, I attempted to determine in the five January litters whether any of the females were pregnant, and if so, how long they had been pregnant. This was done (1) to assess the degree of sexual maturity of the pups and (2) to determine if the aggressiveness of the female pups was associated with their being pregnant. There had been reports (see Marques and Valenstein, 1977) of such an association.

Determination of pregnancy was accomplished by either (1) separating the sexes and waiting sixteen days to see if any female littered, or (2) sacrificing the female and dissecting out the uterus. If embryos were present, I attempted to determine the day of gestation by comparing their appearance with photographs of the embryonic stages in Boyer (1968).

To the best of my knowledge, the above method was accurate to within one or two days, as long as the female was at least seven days pregnant. I could not distinguish between non-pregnant females, and females which may have been six or fewer days pregnant, as the implantation of the embryo is not complete until day six (Boyer, 1968).

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*Obtained from JAMAR Chemical Co., North Andover, Mass.

A Preliminary Study: Effects of Removing the Mother from Cage

I intended to remove the mother from the cage during the main observation sessions on play. Particularly with the younger, smaller pups, the presence of the mother would often obscure whatever was taking place in the nest area. A short preliminary experiment was done to determine if removing the mother would greatly affect the overall activity level of the pups.

The four litters born in October were used for this experiment, which was made when these pups were around 25 days old. Each of the four litters was observed for six 10-minute sessions, three with the mother removed from the cage, and three with her left with the pups.

In each session, the activity of the pups was scored every 30 seconds for the ten minutes. The activity score was the number of animals awake and out of the nest at the 30 second point.

The average activity score was then calculated for each session. A t-test (paired by litter) was performed to determine if there was a significant difference in average activity scores between sessions with the mother removed and sessions with her left in the cage. Results are shown in Table 3. I concluded that removing the mother did not significantly affect the general activity level of the pups ($t = 0.69$; $p > 0.5$).

Table 3. Average activity score of pups: mother removed vs. mother left in cage.

Litter	Activity score (average number of pups awake and out of nest during a 10-minute observation session)	
	Mother removed	Mother left
Helena #1	1.3	4.1
	4.3	1.2
	4.1	2.5
Alice #1	3.3	2.5
	2.1	2.7
	1.7	1.7
Victoria #1	1.8	1.2
	4.3	3.7
	3.7	1.9
Charlotte #1	0.7	2.1
	1.3	1.5
	1.9	1.1

d.f. = 11; t = 0.69 (paired t-test).

Observational Methods

Of major interest to me was the amount of time the pups spent playing (including the length of individual play bouts), the motor patterns involved in their play, and how these both might change over time. I also wished to look at amounts of vocalization and aggression in the litters. Vocalizations were monitored because they commonly occurred during play. Aggression was of interest because it first appeared during the period of observations (when the pubs were about 35 days old) and the subsequent increase in aggressive encounters seemed associated with a decrease in playful interactions.

The above information on the pups' behavior was acquired in two major ways: (1) by using an event recorder and (2) by movie filming.

a. The event recorder

An Esterline-Angus twenty-channel event recorder was employed to obtain the basic data on the pups' play, amount of vocalization, and amount of aggression.

For each of the 41 days (days 14 through 54) when formal observations were to be made, data were collected on a minimum of 10 half-hour observation sessions using the event recorder. Before observations began a schedule to determine which litters were to be observed was set up, and adjusted so that all litters were used for approximately the same number of sessions.

Immediately prior to the start of data collection, the position of the animals (pups and mother) within the cage was marked on a diagram of the cage. Following this, the mother was removed.

The pups' activities were then observed for a half-hour, and recorded via a keyboard which was connected to the event recorder (see Figure 1). To record a vocalization or aggressive encounter, I pushed a key briefly. For play bouts, the key was pressed down for the duration of the bout. Thus, for each half-hour session a record was obtained of (1) the occurrence and length of each play bout, (2) the number of vocalizations, and (3) the number of aggressive encounters.

When possible, I took written notes during these sessions, giving some supplementary comments on the litter's behavior, e.g., "pups have slept for past 10 minutes." I also noted such things as the day the pups' eyes started to open, the first play bouts out of the nest, or when a female appeared to be in estrus.

Finally, for several weeks during observations of the January litters, I recorded the gender of the pups involved in playful and aggressive interactions; i.e., the number of times the interactants were two males, or two females, or one of each.

b. Operational definitions

I used the following operational definition of play in deciding whether or not to record an interaction:

A play bout (1) involved at least two pups, who (2) engaged in a touching interaction in which they were apparently "aware" of

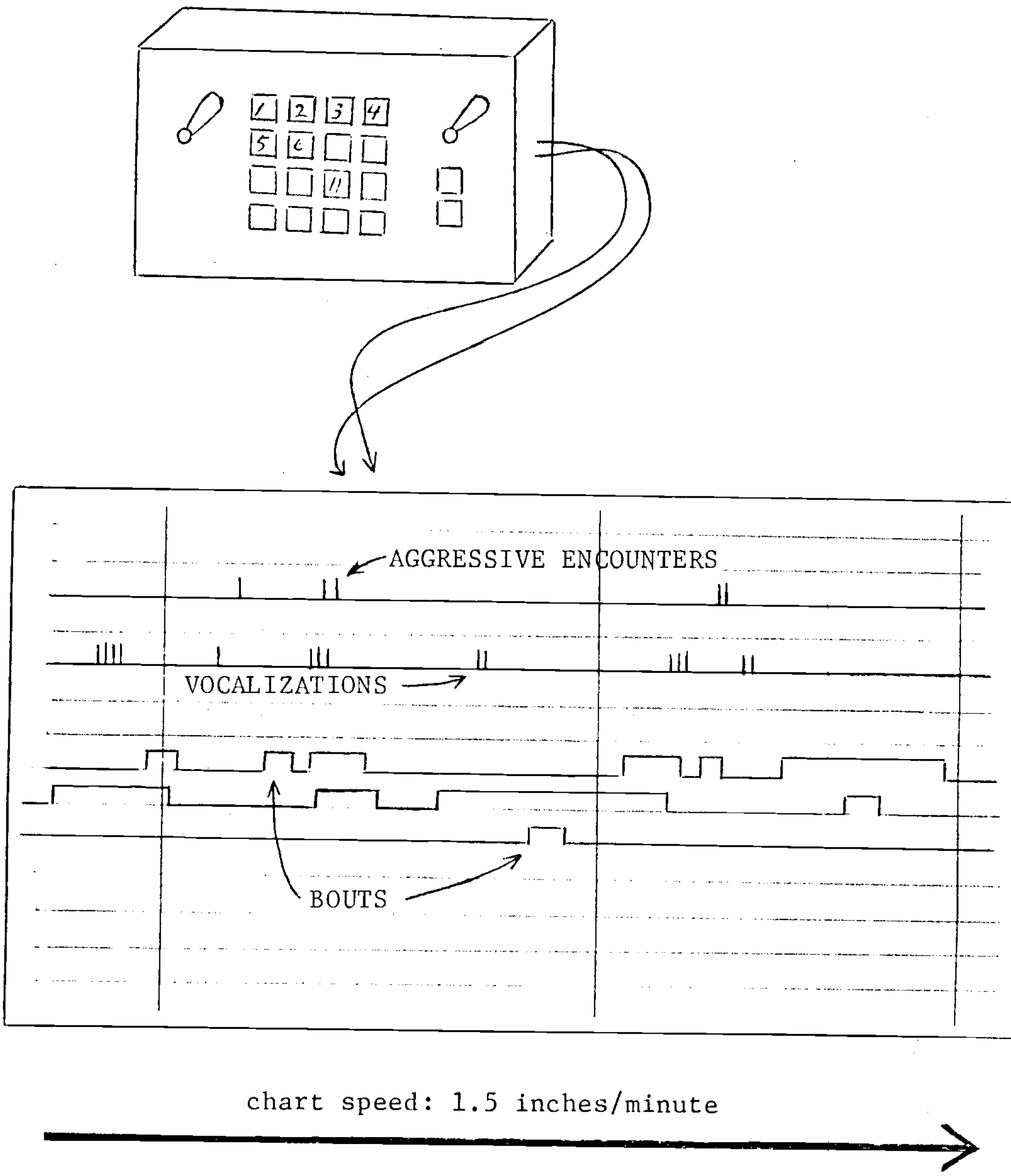


Figure 1. Equipment used in recording observations on play. Shown at the top is the keyboard used to code observations for the event recorder. Below that is a sample event recorder chart.

each other's presence, in that they directed paw or mouth movements towards the partner, and/or appeared to be looking at the partner. The interaction typically involved one or both of the following two general kinds of movements: (a) paw push, and (b) wrestle. (3) The break-off of the playful interaction was not a "hurried one," i.e., the pups did not run away from each other, nor did one run while the other gave chase.

Note that (1) above means that all play recorded was social play. I could recognize no solitary play in these animals, a conclusion which is supported by Dieterlen (1959).

An aggressive encounter was operationally defined as consisting of one or the other of the following sequences:

(1) One pup lunged forward at another, and chased him. The chase was often accompanied by loud vocalizations.

(2) The pups engaged in some of the movements typical of a play bout but the interaction was relatively short, and ended with one pup chasing the other, again typically with loud vocalizations.

The sound referred to as a "vocalization" might be described as a squeak or, in an aggressive context, more like a screech. The only other kind of sound I heard the animals make was "teeth gnashing." This occurred only once or twice, during particularly vicious fights.

c. Movie filming

Movie film was used to record the pups' behavior, so that specific motor patterns used in play could be identified and described in detail. For a closer analysis of behavior, written notes cannot compare with the amount of information that filming provides, and Eible-Eibesfeldt (1975) has written that ". . . motion picture film has become the ethologist's most important means of documentation."

Eight 100 ft. rolls of 16 mm movie film were taken of the litters. The film was shot at 16 frames per second with a 1/125 second shutter speed. I concentrated on one litter in particular (Alice #2), obtaining film at about five-day intervals throughout the period of observations (days 14 to 54).

Reduction of Data and Statistical Methods

a. The event recorder

The length of each play bout was measured from the event recorder chart. The number of vocalizations and aggressive encounters was also counted from the chart.

If two marks on the chart indicated that play episodes were separated by one second or less, they were counted as only one play bout. The one-second figure was somewhat arbitrary, but reflected my experience in watching the animals. If there had been as much as one second between bouts, it was likely that the pups had been involved with some other activity in the meantime; with less than a second, there had probably been no such intervening activities.

The data obtained from the event recorder were averaged over the ten observation sessions for each day of age. Histograms were constructed showing the change in the amount of play, length of bouts, number of vocalizations, and aggression over the 41-day period of development.

In addition, the data on length of bouts were sorted into ten groups, representing days 14-17, 18-21, 22-25, etc. A frequency distribution was then made for each group; the number of bouts being counted by one-second intervals. A survivorship function (the logarithm of number of bouts exceeding a given bout length versus length of bout) was plotted for each group, and a least-squares linear regression line obtained for each plot. These survivorship plots were used in examining certain hypotheses concerning factors which might control the lengths of play bouts (see Results and Discussion).

Other statistical tests were used when appropriate, and are described as needed in Results.

b. Movie film

The movie films were used in describing the motor patterns seen in playful and aggressive encounters. Drawings were made of some of the typical postures and movements. Particular attention was paid to any changes in the form, number, or sequencing of motor patterns during the ontogeny of play. Also of special interest was a comparison of the behavioral elements seen in play with those seen in aggressive encounters.

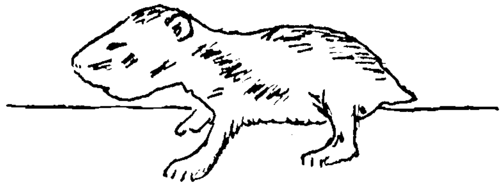
RESULTS

Physical Development during the Period of Observations

Physical growth in the young hamster is rapid (Robinson, 1968). Average weight at birth is slightly greater than 2 g (Kent, 1968). By fourteen days of age, when observations on play began, the pups might weigh about 20 g.

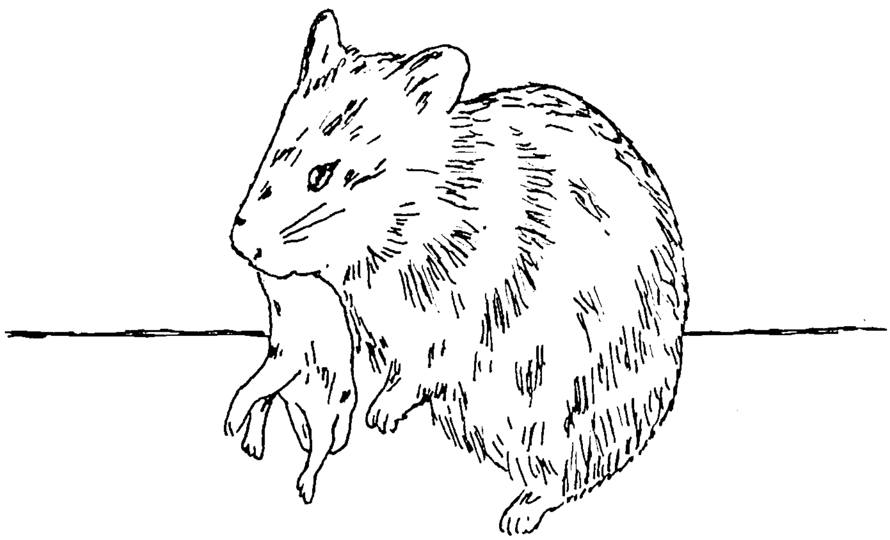
The fourteen-day-old pups were already able to vocalize, chew on food pellets, pouch materials, and perform full-face grooming (the animal places its forepaws behind the ears and brings the paws forward, grooming the entire facial area; it is evidence of a certain minimum amount of coordination). They spend most of their time in the nest with the mother, but are able to leave it, usually for only short periods, and visit corners of the cage to urinate or defecate. They present a rather ungainly appearance (see Figure 2a) and their walking gait seems stiff-legged and awkward.

At 30 days of age, the average weight of the young animals was about 55-60 g. These pups had lost their earlier awkwardness, and looked more like small versions of the adult animal (see Figure 2b). Fifty-five-day-old pups weighed an average of about 105 g, which was close to the average weight of the adult females (130 g). An adult female is shown in Figure 2c for size comparison. The health of all animals was good throughout the period of observation.



(a). 14 day old pup

(b). 30 day old pup



(c). Adult female, carrying young pup in mouth

Figure 2. The golden hamster at various ages. Traced from 35 mm slides, approximately to the same scale.

The Development of Play Behavior

The first play was recorded on day fourteen for three of the litters (Trixie, Victoria #2, Charlotte #2); other litters were not seen playing until day 15, or day 16 at the latest. This agrees with the data given by Daly (1975) who saw the first "swatting play-fights" between his golden hamster pups at a median age of 14 days (earliest was 13 days), and "full playfights" two days later (median, 16 days; earliest, 15 days). Dieterlen (1959) mentions that younger pups -- eleven to twelve days old -- are induced to "play" by the nursing mother licking them in the stomach. I did not observe this behavior in my litters.

For the first few days, all play was within the nest area, even though several pups were often out of the nest at one time. The first play out of the nest was seen on day 17, and was perhaps related to the pups' eyes starting to open the day before. With their eyes closed, the animals seemed "unaware" of each other, and a bout could start only after phyiscal contact, unlikely outside the confines of the nest.

Figure 3 shows the mean total time spent playing in a half-hour session, from fourteen days of age to day 54. There was little play in the fourteen and fifteen-day-old litters. The amount then increased rapidly until just three days later, day 18, play had reached the (relatively) high level at which it plateaued, and remained at until around day 35. At this plateau level, the pups were spending an average of 300 to 400 seconds (about five to seven

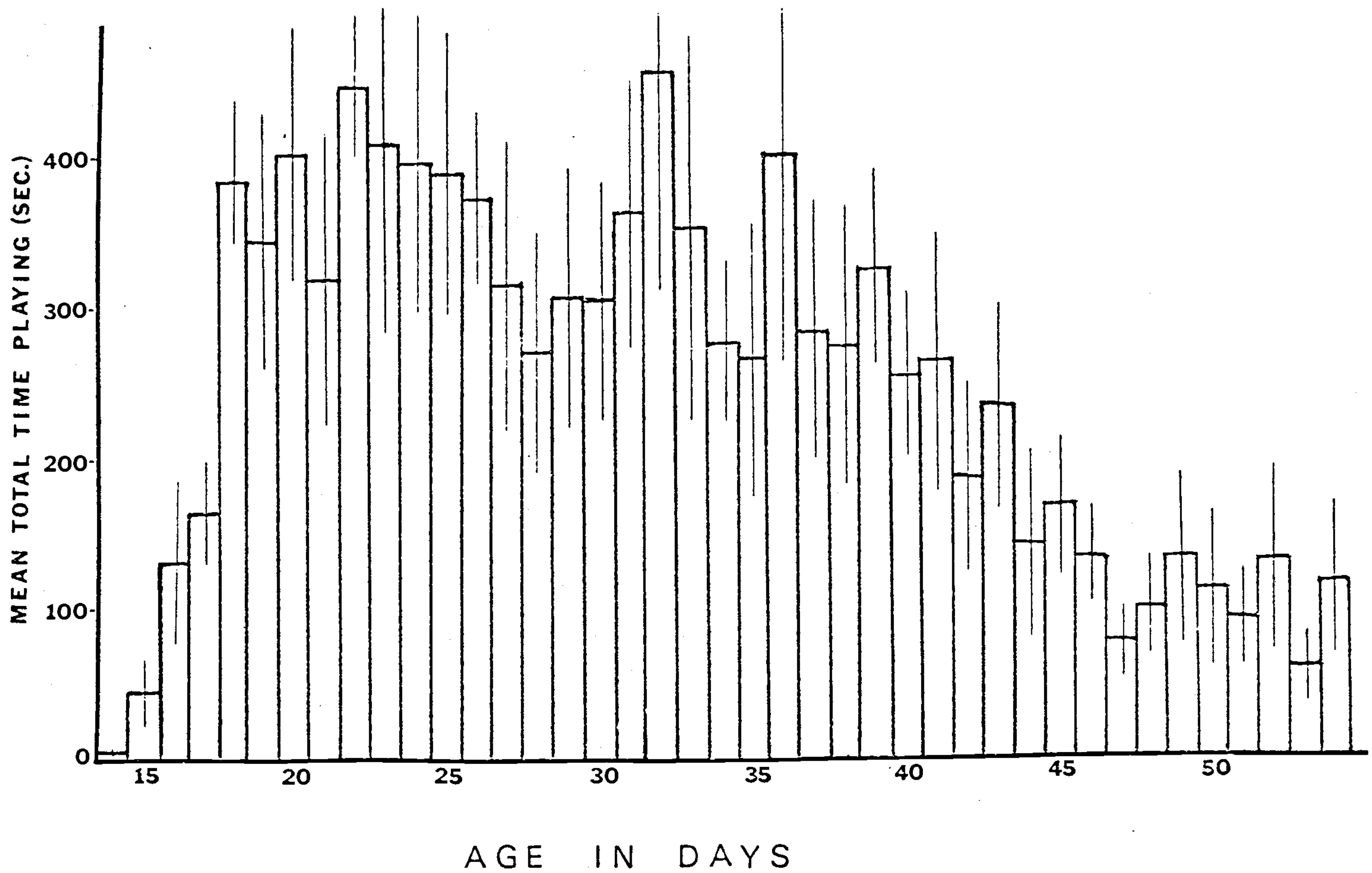


Figure 3. Average total time spent playing per half-hour observation session, by day of age. Vertical lines indicate ± 1 standard error of mean.

minutes) per half-hour session in play. Note that this figure is for all the pups in a litter taken together; an individual animal would not spend that much time playing.

After about day 35, the amount of play began to decline. Particularly after day 50, play bouts became sporadic, and so increasingly aggressive in nature that it was difficult to know whether to score a given interaction as play or as a serious attack.

The span of time during which the pups play is thus from 14 days of age until approximately 50 to 55 days (seven to eight weeks). These ages form a somewhat longer period of play than had been previously noted for the hamster by Rowell (1961), who stated that play in this species was typical of the time between three and six weeks of age.

The average number of bouts per session is shown in Figure 4. The number of bouts shows a generally similar pattern over the developmental period as the total time spent playing.

Within each day there could be considerable variation in the amount of play seen from one session to another. Occasionally, there was no play at all during the observation period. On other occasions, the pups would play almost continuously for the entire half-hour. I recorded as much as 1360 seconds (almost 23 minutes) of play during one session (Charlotte #2, 32 days old), and as many as 83 bouts (Victoria #2, 27 days old). There were several other sessions with nearly as much play. The wide variation in time spent playing is reflected in the relatively large standard errors seen in Figures 3 and 4.

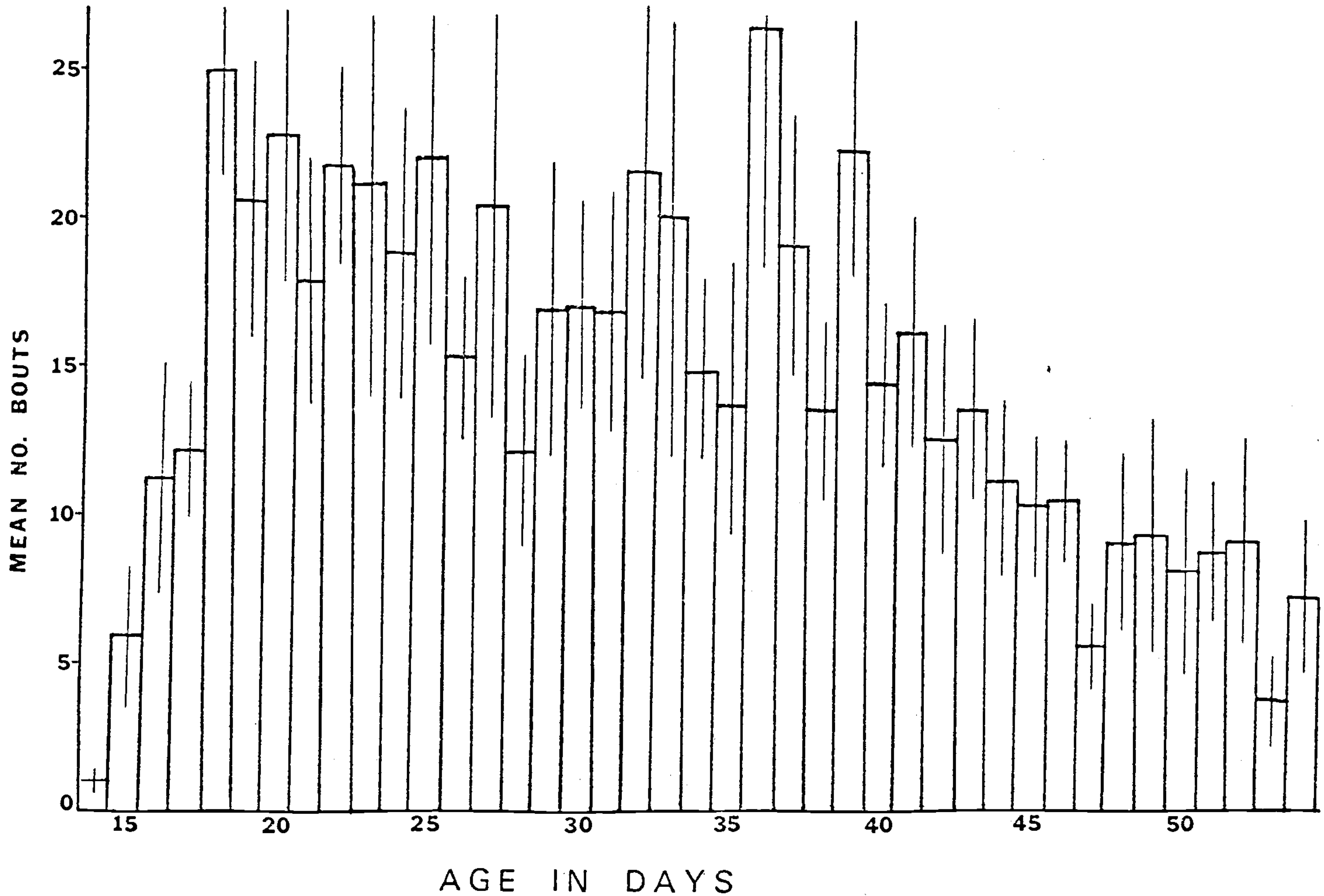


Figure 4. Average number of bouts per half-hour observation session, by day of age. Vertical lines indicate ± 1 standard error of mean.

Figure 5 shows the change in average length of an individual play bout from day 14 to day 54. Bouts during the first few days were considerably shorter than those occurring later. After approximately day 22, the length of bout plateaued and then decreased slightly after days 35-40.

Survivorship Functions of Bout Length

The equations of the least-squares linear regression lines obtained for each survivorship function are given in Table 4. Note that the equations are in the form $\hat{y} = a(b)^x$, where $\hat{y}$ = the predicted number of bouts greater than duration x. The y intercept is represented by "a," and "b" is the probability of a bout continuing for longer than duration x. A straight line on the semi-log plot would therefore indicate that the probability of a bout ending was a constant and independent of how long the bout had lasted (Slater, 1974). Such independence would be expected if play bouts continued until interrupted, the interrupting events being random with respect to the occurrence of play (McDonald, 1977).

Three examples of the survivorship functions and accompanying linear regression lines are shown in Figures 6, 7, and 8. Days 14-17 represent the first few days of play; days 30-33, the middle period during which the average bout length was relatively long; and days 50-54, the last few days of play.

The ordinate on these graphs was scaled so that the plots all start at the same place on the y axis. The shape of the plots can

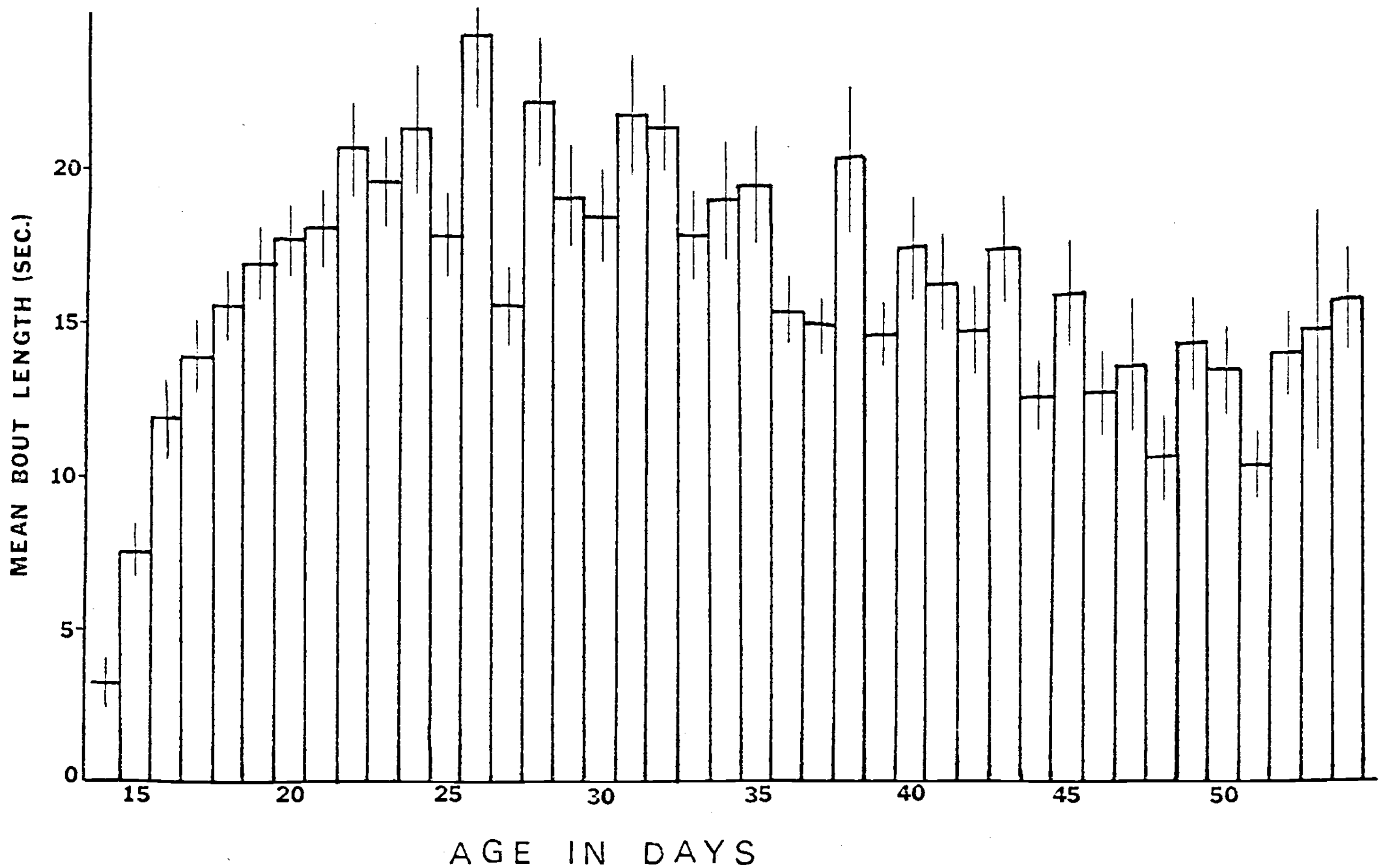


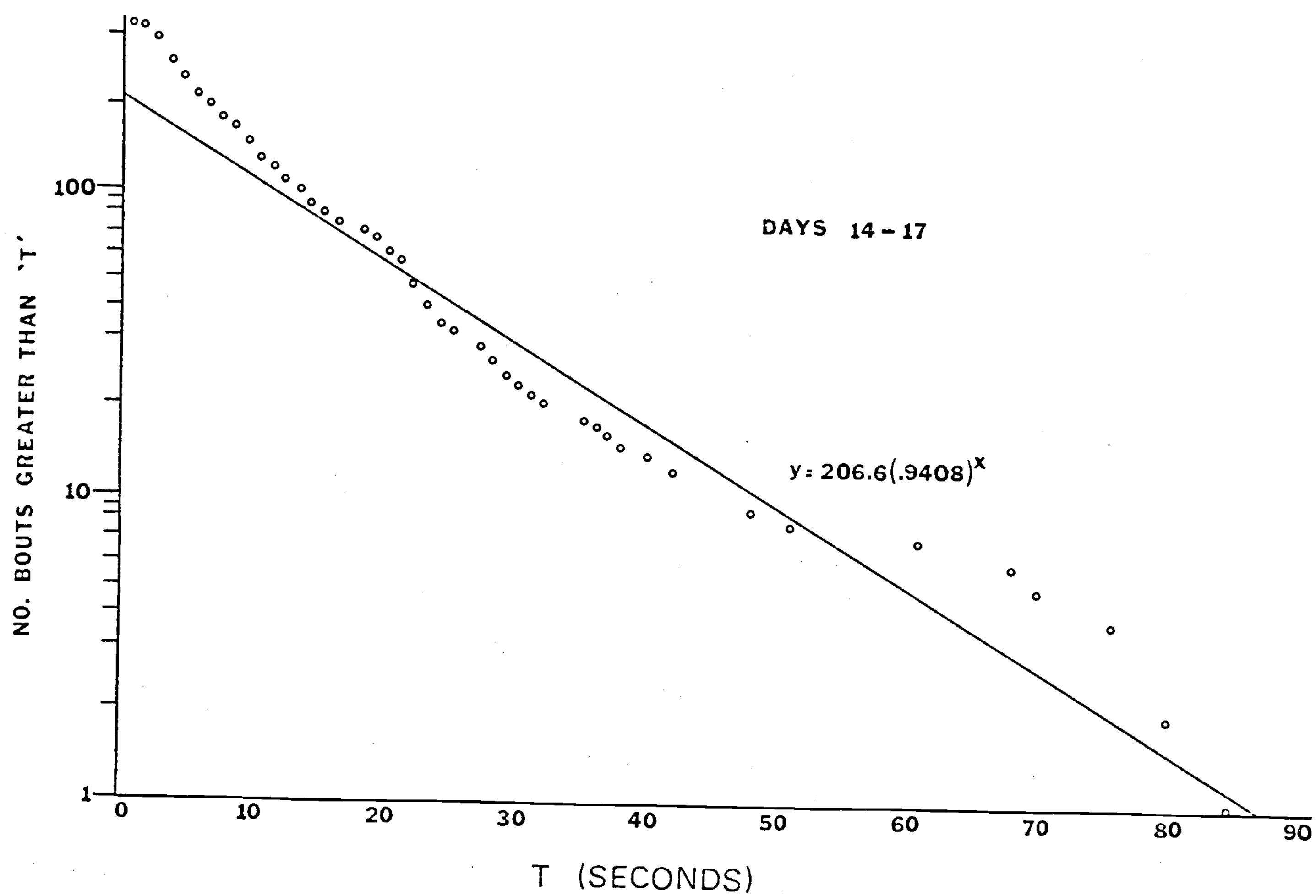
Figure 5. Average length of play bout, by day of age.
Vertical lines indicate ± 1 standard error of the mean.

Table 4. Survivorship functions: equations for the least-squares linear regression line.

Group	Number of bouts	Least-squares line*
Days 14-17	317	$\hat{y} = 206.6\ (0.9408)^x$
Days 18-21	909	$\hat{y} = 617.6\ (0.9557)^x$
Days 22-25	852	$\hat{y} = 523.5\ (0.9649)^x$
Days 26-29	680	$\hat{y} = 376.2\ (0.9680)^x$
Days 30-33	750	$\hat{y} = 578.5\ (0.9585)^x$
Days 34-37	737	$\hat{y} = 459.0\ (0.9570)^x$
Days 38-41	664	$\hat{y} = 362.2\ (0.9623)^x$
Days 42-45	477	$\hat{y} = 381.4\ (0.9471)^x$
Days 46-49	357	$\hat{y} = 251.8\ (0.9423)^x$
Days 50-54	375	$\hat{y} = 232.5\ (0.9460)^x$

*The equations, originally in the form $y = mx + b$ (where y is the log of the number of bouts), were transformed by taking the anti-log of each side.

Figure 6. Survivorship function of bout lengths, with least-squares linear regression; days 14-17.



DAYS 14 - 17
y = 206.6(.9408)x
NO. BOUTS GREATER THAN 'T'
100
10
1
0
10
20
30
40
50
60
70
80
90
T (SECONDS)

Figure 6.

Figure 7. Survivorship function of bout lengths, with least-squares linear regression; days 30-33.

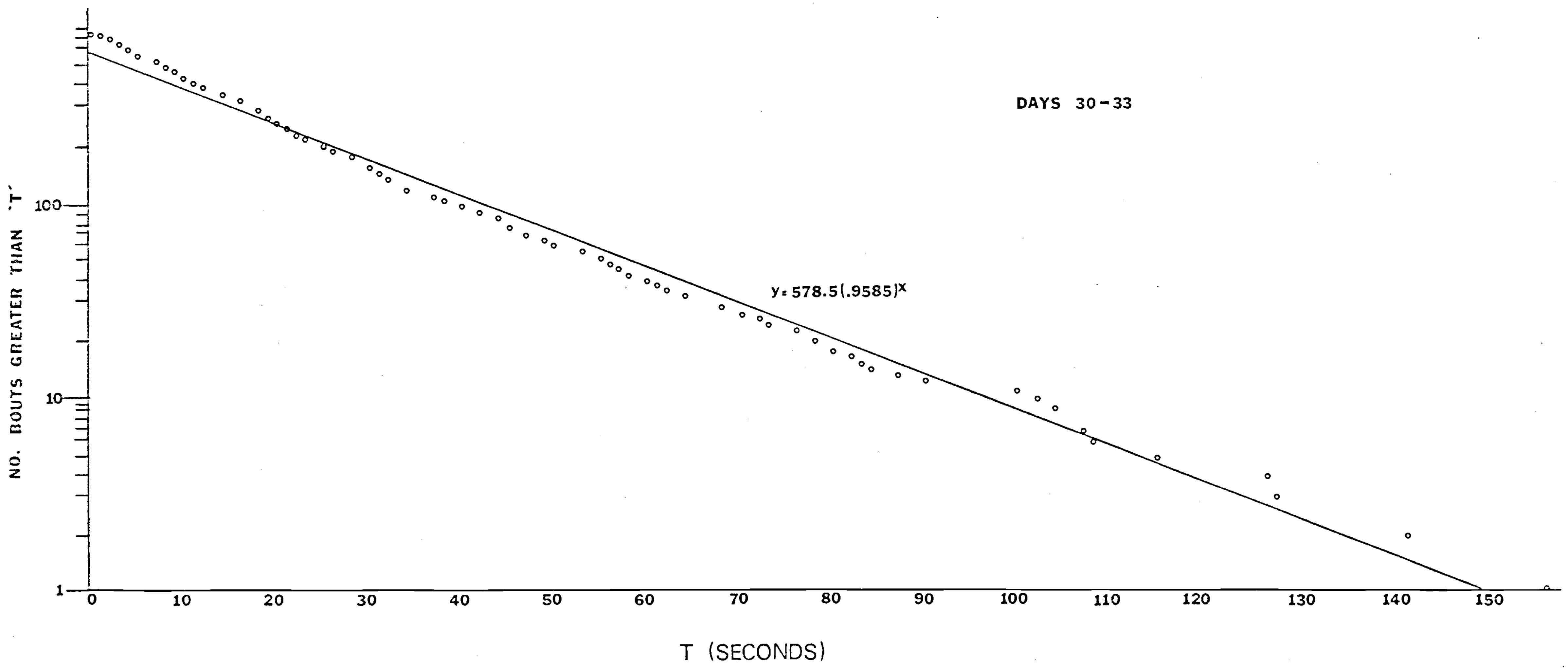
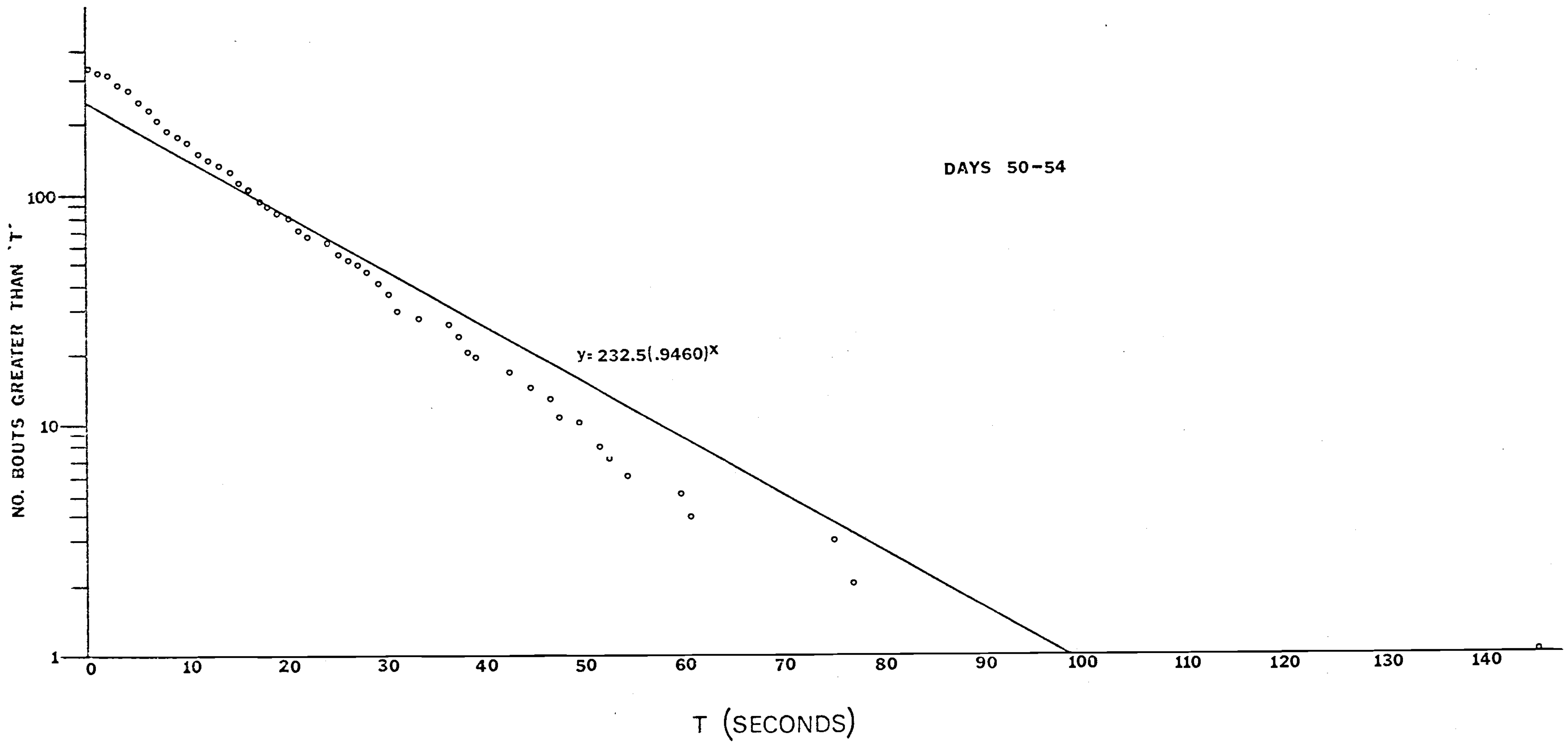

DAYS 30-33
y = 578.5(.9585)^x
NO. BOUTS GREATER THAN 'T'
T (SECONDS)
1
10
100
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150

Figure 8. Survivorship function of bout lengths, with least-squares linear regression; days 50-54.


DAYS 50-54
y= 232.5(.9460)^{x}
NO. BOUTS GREATER THAN 'T'
100
10
1
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
T (SECONDS)

then be compared visually, even though the absolute number of bouts involved is different in each case.

A comparison shows that the slope of the least-squares line is relatively steep for bouts during days 14-17 and days 50-54, and considerably flatter for days 30-33. This is reflected in the regression equations, which show that "b" tends to be smaller for the earlier and later groups, larger for the middle ones. With a larger "b" the probability of a bout continuing past a given time T is higher, and thus the probability of the bout ending lower.

Visual inspection of Figures 6, 7, and 8 shows the plotted values to be close to a straight line but with a consistent lack of fit; in each case the actual data points first overshoot, then undershoot, and finally again overshoot the calculated line, forming a slight concave curve.

A Chi-square test (described in Slater, 1974) was used to check the apparent lack of fit. In this test, the intervals of bout durations within which one-fourth of all bouts should occur is calculated from the regression line. The actual number of bouts observed to occur in each interval is then compared to the predicted value.

Table 5 gives the results of the Chi-square tests, which confirm what was suggested by visual survey. In each case, there was a significant lack of fit between the plotted data and the least-squares line. Inspection of Table 5 shows that this lack of fit was due mainly to (1) more short bouts being observed than

Table 5. Chi-square test for goodness of fit of regression lines.

Group	Intervals of bout duration within which 1/4 of observed bouts should fall	# Bouts Observed	# Bouts Expected	χ^2 and p (3 df)
Days 14-17	0- 5 sec	122	79.25	$\chi^2 = 42.4$
	5-11	87	79.25	
	11-23	64	79.25	$p < .005$
	23+	44	79.25	
Days 18-21	0- 6 sec	300	227.25	$\chi^2 = 56.7$
	6-15	257	227.25	
	15-30	203	227.25	$p < .005$
	30+			
Days 22-25	0- 8 sec	300	213	$\chi^2 = 94.1$
	8-19	259	213	
	19-38	174	213	$p < .005$
	38+			
Days 26-29	0- 9 sec	277	170	$\chi^2 = 144.2$
	9-21	201	170	
	21-43	137	170	$p < .005$
	43+	65	170	
Days 30-33	0- 7 sec	217	187.5	$\chi^2 = 34.7$
	7-17	220	187.5	
	17-33	193	187.5	$p < .005$
	33+	120	187.5	
Days 34-37	0- 7 sec	259	184.25	$\chi^2 = 71.6$
	7-16	215	184.25	
	16-32	155	184.25	$p < .005$
	32+	108	184.25	
Days 38-41	0- 7 sec	273	166	$\chi^2 = 128.4$
	7-18	186	166	
	18-35	129	166	$p < .005$
	35+	76	166	
Days 42-45	0- 5 sec	157	119.25	$\chi^2 = 28.5$
	5-13	138	119.25	
	13-25	95	119.25	$p < .005$
	25+	87	119.25	

Table 5 (Continued)

Group	Intervals of bout duration within which 1/4 of observed bouts should fall	# Bouts Observed	# Bouts Expected	χ^2 and p (3 df)
	0- 5 sec	119	89.25	$\chi^2 = 34.5$
Days 46-49	5-12	114	89.25	
	12-23	69	89.25	$p < .005$
	23+	55	89.25	
	0-5	113	93.75	$\chi^2 = 26.5$
	5-12	120	93.75	
	12-25	85	93.75	$p < .005$
	25+	57	93.75	

expected and (2) fewer long bouts observed than expected. Thus, the probability of a bout ending is not independent of bout duration, but is slightly higher than that predicted by the regression equation for shorter bouts, and somewhat lower for the longer ones. The probability of a bout ending is also dependent on the age of the pups, which was seen in comparing the different slopes of the regression lines.

Gender Preference in Play

There was originally no reason to suspect that pups might choose their play partners other than at random with respect to sex. Data gathered on the genders of playing pairs indicated, however, that some combinations showed up in numbers different from what would have been predicted by chance. A Chi-square analysis was used to test whether the pups were choosing their play partners randomly with respect to gender. Table 6 summarizes these results, including a breakdown of frequencies according to litter and age of the pups. Taking all litters and all ages combined, there was a tendency for males to play more with other males, and less with females, than expected. Females played with other females at very close to the expected frequency.

Breaking the data down by age and litter complicates the situation, and in some cases the trends just mentioned are reversed. The following generalizations can nevertheless be made:

(1) Using the totals for individual litters, in all cases males played less with females than expected.

Table 6. Number of play bouts between two males, between a male and a female, and between two females; observed and expected frequencies.

	# Male/Male Bouts		# Male/Female Bouts		# Female/Female Bouts			χ^2	
Litter*	Obs	Exp	Obs	Exp	Obs	Exp	$\sum$	(2 df)	p
Victoria #2									
days 41-46	78	62.9++	52	62.9	2	6.3	132	8.4	$p < .025$
days 47-54	79	68.1	64	68.1	0	6.8	143	8.8	$p < .025$
total	157	131.0	116	131.0	2	13.1	275	16.3	$p < .001$
Trixie									
days 38-44	6	2.9	25	29.0	30	29.0	61	3.9	$p < .1$
days 45-54	0	2.7	19	26.7	37	26.7	56	8.9	$p < .025$
total	6	5.6	44	55.7	67	55.7	117	4.8	$.05 < p < .1$
Charlotte #2									
days 41-46	1	3.0	43	30.5	20	30.5	64	10.1	$p < .01$
days 47-54	2	3.2	12	31.9	53	31.9	67	26.8	$p < .001$
total	3	6.2	55	62.4	73	62.4	131	4.4	$.05 < p < .1$
Alice #2									
days 32-40	17	15.4	60	61.7	31	30.9	108	0.2	---
days 41-46	19	14.4	47	57.7	35	28.9	101	4.7	$.05 < p < .1$
days 47-54	49	10.0	13	40.6	9	20.3	71	175.9	$p < .001$
total	85	40.0	120	160.0	75	80.0	280	60.9	$p < .001$
Grand total	251	182.7	335	409.1	217	211.2	803	85.4 (8 df)	$p < .001$

*This data is available for four of the nine litters only. Victoria's litter had 5 males, 2 females; Trixie and Charlotte's litters had two males, 5 females; Alice's litter had 3 males, 4 females.

++'Expected' values may not add up precisely, due to rounding errors. The method used in obtaining these values is given in the appendix.

(2) Taking the litters individually, in most cases the Chi-square value increased with the age of the pups, meaning that older pups deviated more than younger pups from expected frequencies. This increased deviation with age was sometimes quite marked, resulting in p values of less than .001 for the last week of observations. In the one litter for which there are data on pups younger than 41 days (Alice #2) the observed frequencies for play bouts during days 32 through 40 correspond almost exactly to the expected values. In this same litter Chi-square is almost significant ($.1 < p < .05$) for bouts during days 41 to 46, and extremely large for days 47-54.

Aggressive Encounters

The first occurrence of a clearly aggressive encounter ("lunge-attack") was noted in two litters (Helen #1 and Alice #1) at 34 days of age. Aggression was not observed in the remaining seven litters, however, until days 40-45. Figure 9 shows the sharp increase in average number of attacks per session after day 40.

a. Aggression and the onset of sexual maturity

Aggression in the golden hamster has received considerable attention because of the anomalous situation that the female is the most aggressive sex (Payne and Swanson, 1970, 1971; Marques and Valenstein, 1977). The results of this study are in agreement: all attacks seen during an observation session were initiated by female pups (although outside of the sessions I did see a single instance of a male attacking another male.)

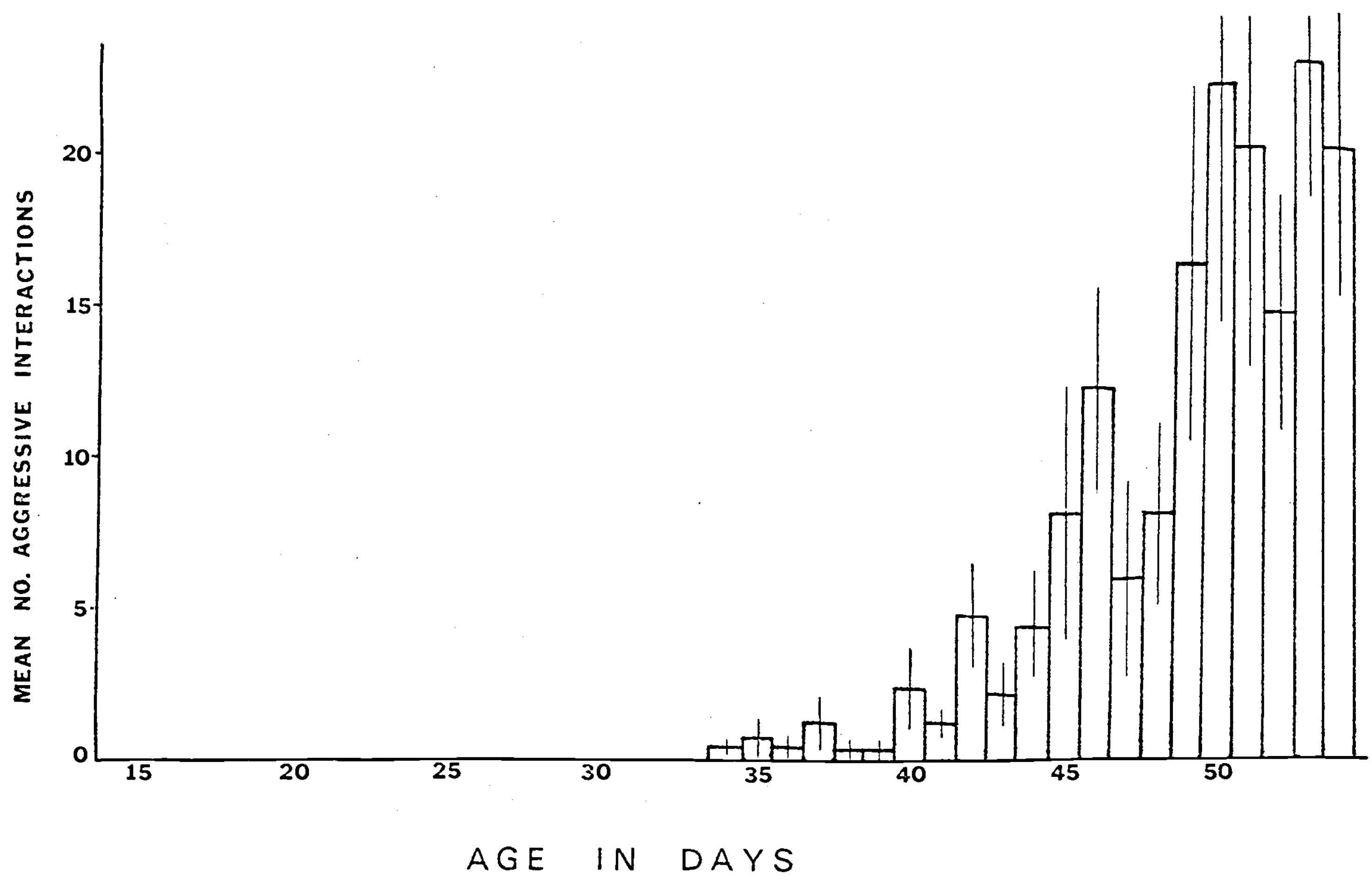


Figure 9. Average number of aggressive interactions per half-hour observation session, by day of age. Vertical lines indicate ± 1 standard error of the mean.

I also noted that the females first came into estrus at about the same time as the initial aggressive encounters. The first instance of lordosis with mounting was seen on day 37 (Helena #2); it was also seen in several other litters within the next few days. Mounting in the younger pups was often mis-oriented and generally did not result in successful copulation; nevertheless, many of the females did become pregnant prior to the end of observations on day 54.

Table 7 shows (1) the day on which aggression was first noted in individual female pups and (2) the day of conception, if the pup was later determined to be pregnant. Apparently, pregnancy was not causing the appearance of aggression in these females, as most of the pups, including especially dominant ones, had been aggressive before they were pregnant. It is still possible that some females, unknown to me, had aborted earlier litters. This would make the determination of day of conception inaccurate. However, I feel that this was unlikely to have happened in as many instances as observed.

b. Gender preferences in female aggression

I had noted that certain female pups were particularly dominant in aggressive encounters (the "bullies"). I also noted that aggressive females tended to discriminate between the sexes in their attacks. Some females attacked males almost exclusively, directing little if any aggression towards members of their own sex. Other aggressive animals attacked other females preferentially.

Table 7. Day of first observed aggression and of conception for individual female pups.

Litter	Pup	First aggression	Conception
Alice #2	DW,1	40 days old	53 days old
	DP1,1	43	50
	DW,2	45	49
	DP1,2	46	56-57
Victoria #2	Cinna++	40	47
	DW,0	53	*
Helena #2	SH++	41	48-49
	DW,0	52	48-49
	DW,1(W)	no aggression observed	not pregnant, or less than 6 days PG
	DP1,1		
	DW,1(D)		
Charlotte #2	DW,2	45	not PG, or less than 6 days PG; conception not earlier than 51 days of age
	DW,1(D)	47	
	DP1	45	
	CW	46	
	DW,1(W)	no aggression observed	
Trixie	CW++	40	52-53
	CP1	42-43	48-49
	DP1	no ag. observed	45
	DW(1)	50	not PG, or less than 6 days PG; conception not earlier than 52-54 days of age
	DW(2)	no ag. observed	

*Data missing
++Very dominant individual

A Chi-square test was used to examine the hypothesis that females tended to direct aggression at either males or other females more than would be expected by chance. Table 8 gives the results. In three of the four litters, females showed a very significant tendency to attack males. In the fourth litter (Victoria #2) there was an equally significant tendency for females to attack other females.

This last litter was also unusual in that it consisted of five males and only two females, the highest male to female ratio in the nine litters. The majority of attacks in this litter were by one female ("Cinna") against the other. In this connection Marques and Valenstein (1977) found that adult female hamsters showed marked differences in the level of aggression directed against males. In their study, some females were highly aggressive towards all males, while other females were aggressive towards none; these latter animals were, however, highly aggressive towards other females.

Vocalizations

The average number of vocalizations (squeaks) per observation session is shown in Figure 10. The relationship between amount of squeaking and the age of the pups seems to be more complex than that between age and the amount of play. There were two periods with relatively high levels of vocalization; around days 18 to 25, and after about day 45. In between, especially from day 30 to day 40, there was a definite decrease in squeaking.

Table 8. Number of times females attacked males vs. number of female-female attacks; observed and expected frequencies.

Litter*	Female → Male Observed	Female → Male Expected++	Female → Female Observed	Female → Female Expected	$\sum$	χ^2 (1 df)	p
Alice #2 (data from days 40-54)	218	159	100	159	318	43.8	$p < .001$
Trixie (days 40-54)	217	96.3	72	192.7	280	226.7	$p < .001$
Charlotte #2 (days 45-54)	341	129.7	48	259.3	389	516.6	$p < .001$
Victoria #2 (days 40-54)	36	118.3	106	23.7	142	343.6	$p < .001$

*This data is available for four of the nine litters only.

++The method used in obtaining expected frequencies is given in the appendix

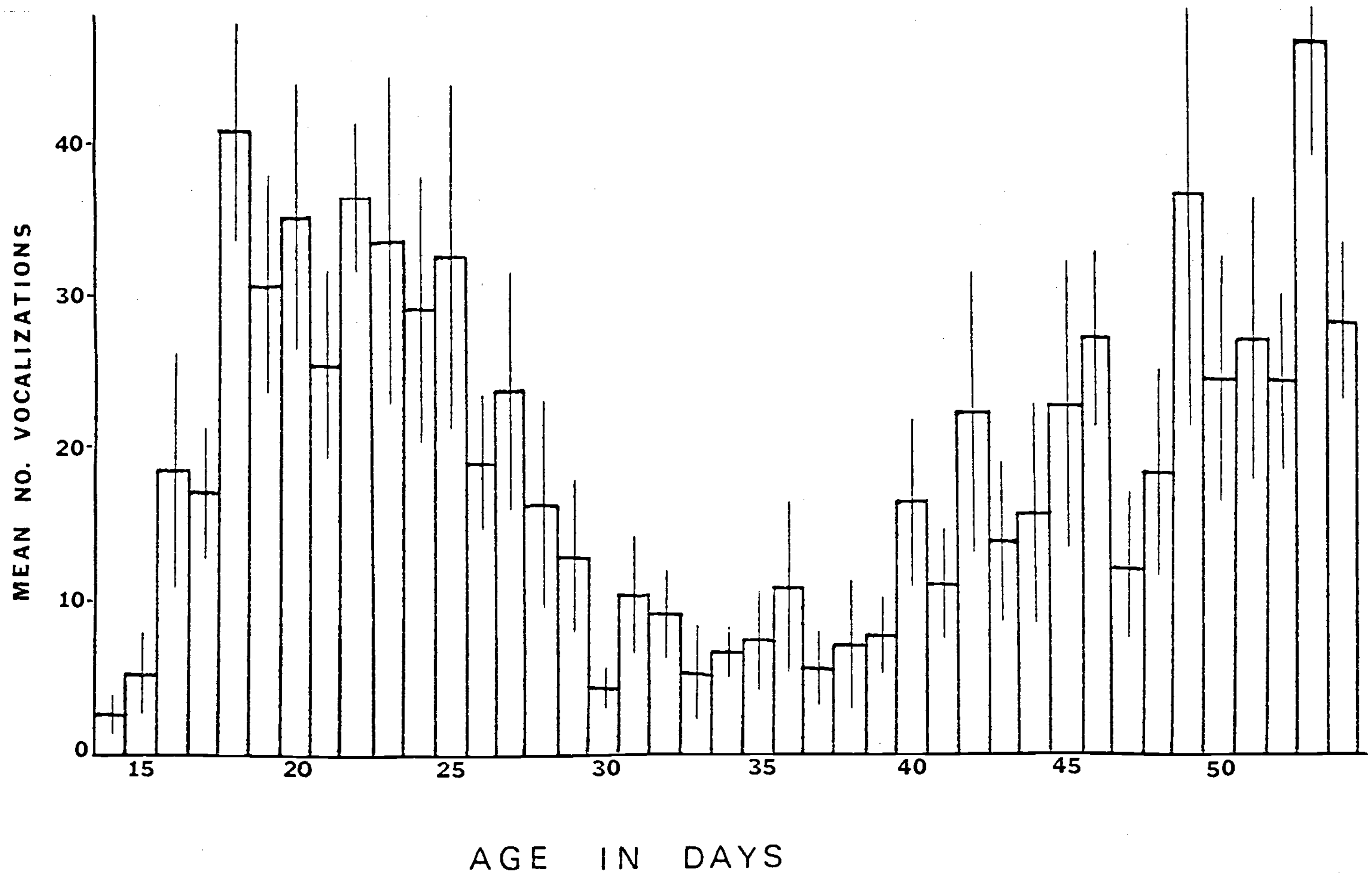


Figure 10. Average number of vocalizations per half-hour observation session, by day of age. Vertical lines indicate ± 1 standard error of mean.

Until day 34, when the first clearly aggressive interactions were recorded, virtually all vocalizations occurred during play. The pups also squeaked during aggressive encounters, however, and the increase in vocalization after day 35 is associated with the first appearance and subsequent increase in aggression.

The Development of Motor Patterns in Play

The behaviors seen in play were few and simple at first, becoming more complex as motor patterns were added to the bout repertoire during ontogeny. Some of the original behavioral sequences were altered gradually as the pups grew older, and patterns common in young pups might be relatively rare in the other animals. The development of these patterns was consistent among litters, and it became possible for the observer to predict what the next stage in play behavior would be.

Play bouts in the youngest pups (14 to 16 days old) took place almost exclusively in the nest area. The first motor patterns seen consisted of two simple variants on a theme:

(1) The pups would use forepaws to push at each others face, while lying face to face on their sides. This was called "prone-paw, on side."

(2) The pups would paw at the facial region as above, but with the partners in a sitting position ("sitting-paw").

I noted that even these youngest pups were capable of vocalizing quite audibly, and they did so during play, although not as frequently as they would a few days later.

It was often difficult to decide which pups were taking part in the first nest area bouts; two animals playing seemed to induce others nearby to do the same, and soon there might be five or six animals pawing somewhat indiscriminately at each other. Figure 11 shows nest area pawing bouts in 16-day-old pups.

By approximately 19 days of age play occurred more commonly outside the nest, and usually involved only two pups at a time. Rarely, a third pup would join in, but bouts including more than two interactants quickly broke up. It was also noticed that out-of-nest play usually occurred in the corners of the cage, or at least close to one wall, and relatively seldom in the middle of the cage area. These "play corners" had been mentioned by Rowell (1961).

The bouts occurring out of the nest included the play behaviors seen before, especially the prone-paw (Figure 12a). Other motor patterns were soon added to the bouts.

One of the first added patterns was the "inhibited bite," which throughout ontogeny was seen in the context of pawing to the face. As the animals pawed, they would move their heads back slightly and hold the mouth open, as if wanting to bite at their partner's face, but restraining themselves.

Even in pups, the inhibition applied to the facial region only, as another pattern soon added was the "mutual bite," seen by 19 days of age. In this behavior, two pups would become locked in a position where they were apparently biting at each other's stomach region (Figure 13a). Neither animal would seem to dominate the encounter, although as the pups got slightly older (20-25 days)

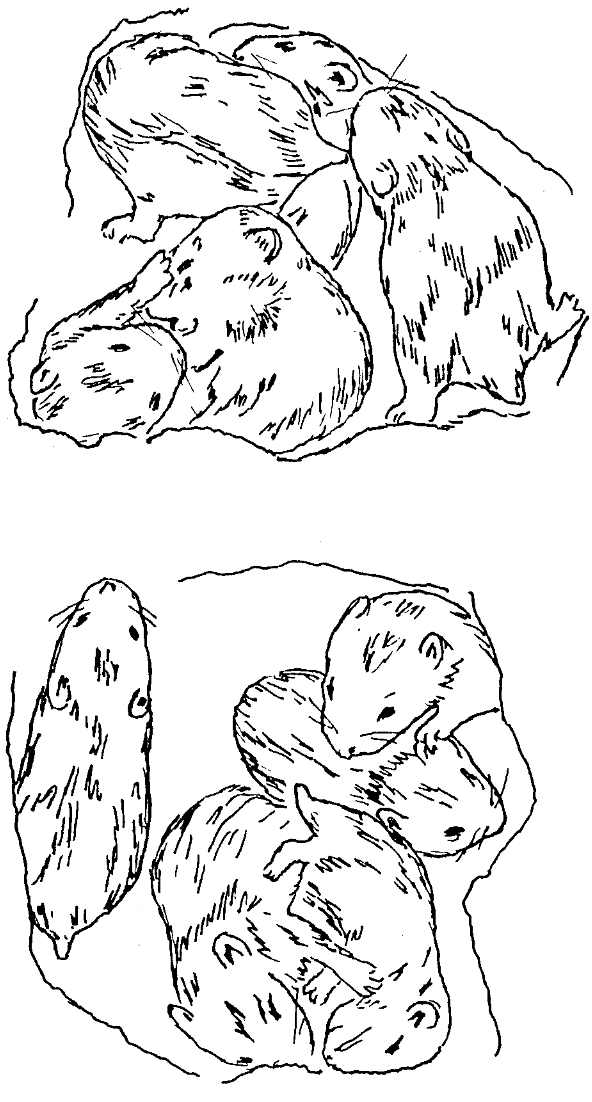


Figure 11. Pawing bouts in the nest area
(16 day old pups). Traced from 16 mm movie film.

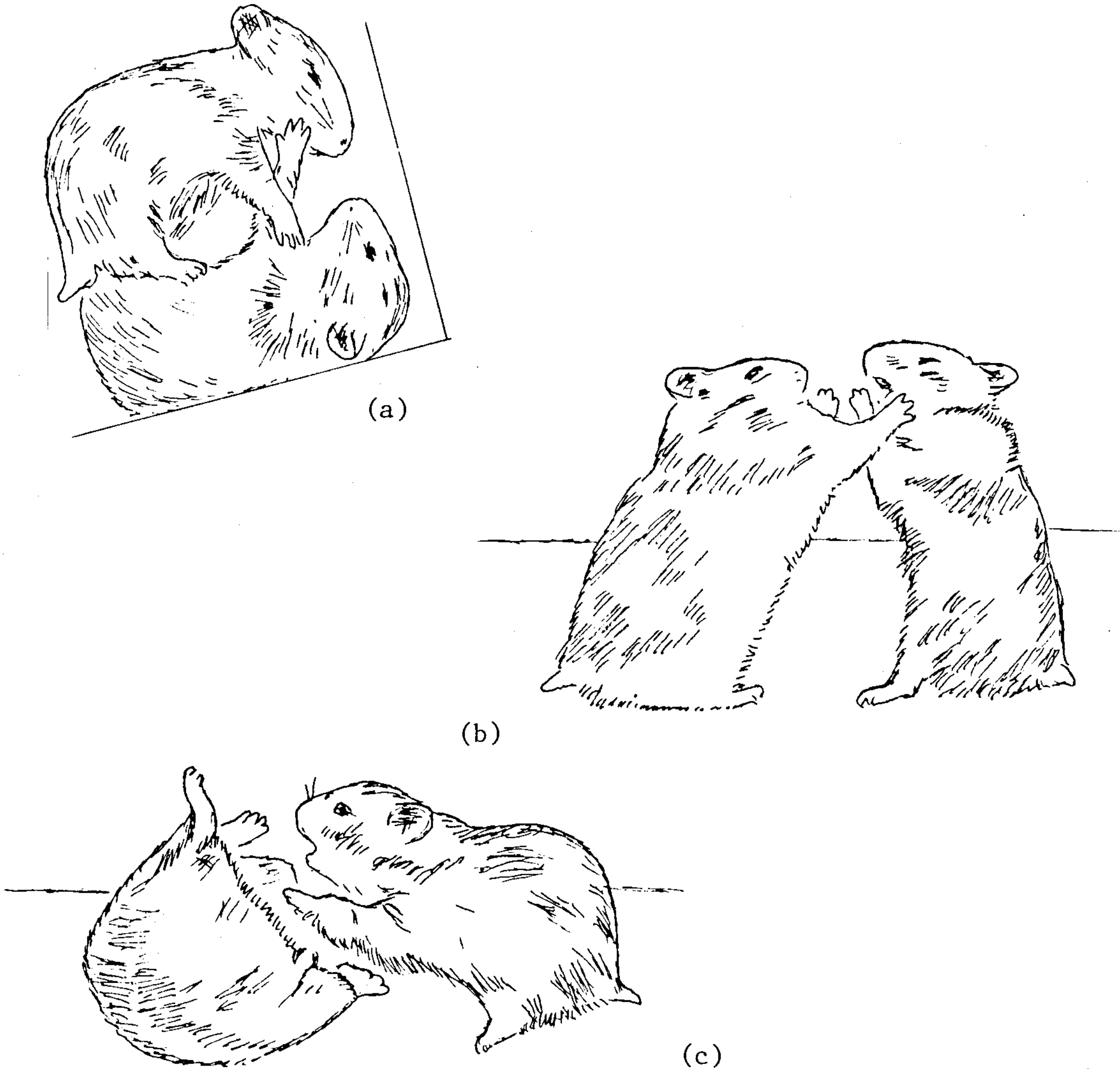


Figure 12. Some motor patterns in play.

(a). "Prone-paw" (19 day old pups). This shot was taken looking down into the cage.

(b). "Stand-up paw" (29 day old pups).

(c). "Pounce" (29 day old pups).

Traced from 35 mm slides and 16 mm movie film.

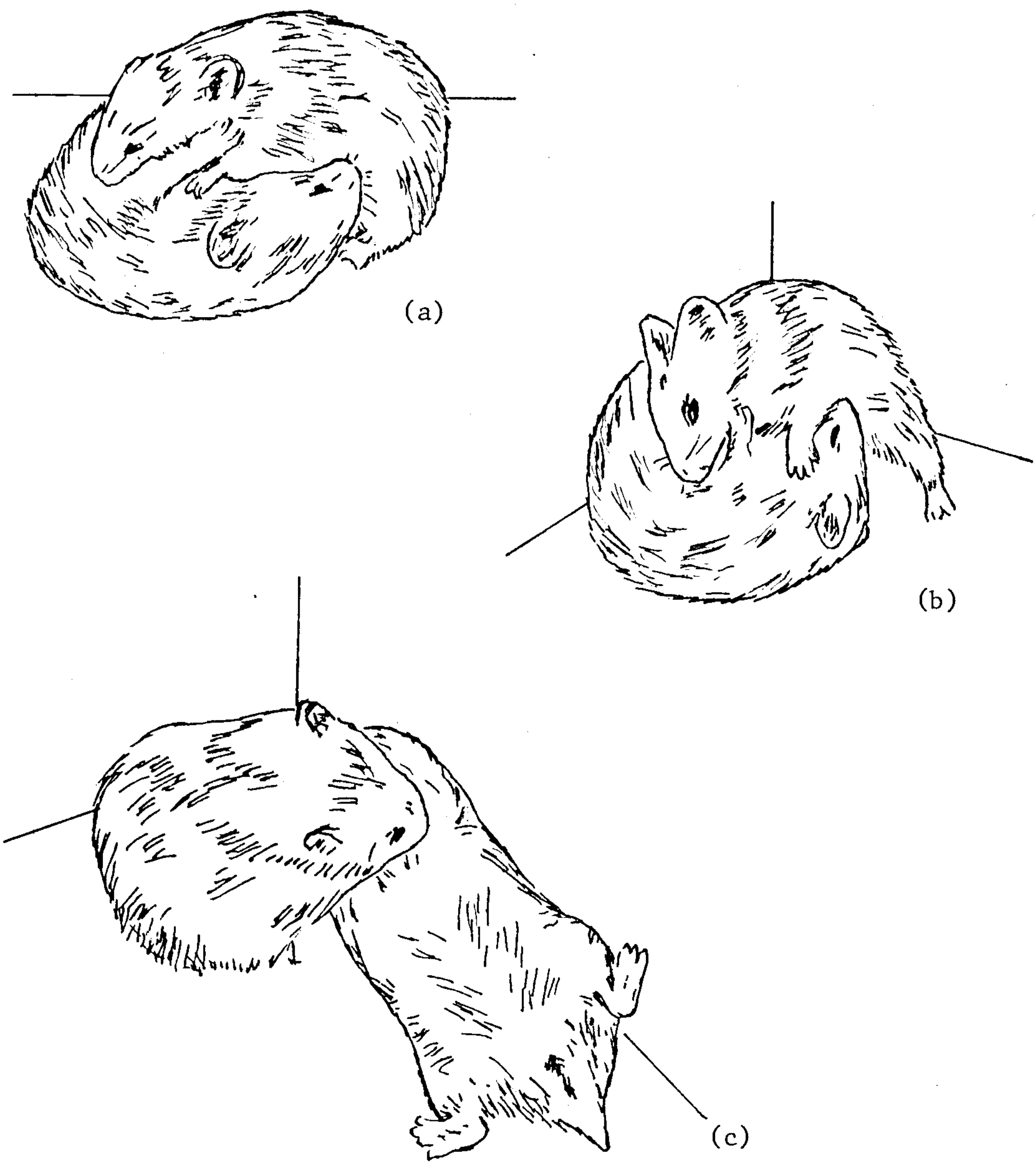


Figure 13. Three forms of play-wrestling.

(a). "Mutual-bite" (18 day old pups)
(b). "Pin" (20 day old pups)
(c). "Wrestle-head" (41 day old pups)

Traced from 35 mm slides and 16 mm movie film.

it was noticed that a play bout would often end immediately following some very loud squeaks, which were perhaps indication of antagonism between the interactants.

Also added to the play repertoire at about this time was the "stand-up paw" (Fibure 12b). This posture is common in the play of several species and was termed "play-boxing" by Poole and Fish (1975; paper on laboratory rats and mice), and "rearing" or "shake-hand posture" by Steiner (1971; Columbian ground squirrels). In the hamster, when the stand-up paw occurred, it was typically the first behavior of a play bout.

Occasionally, one pup would be seen to "pounce" on another during play (Figure 12c). This was most often observed during wrestling; one animal would pull back slightly from the other and then come back down with forepaws extended. Pouncing was seen from about day 18 on, but was never a very common behavior.

In pups younger than about 20 days, there were no clear instances seen of one animal attempting to elicit play from another. However, the pups did groom each other, and as they got older (22 days +) grooming often led to play.

Two kinds of grooming were most effective in beginning a bout. In "ear-pulling" one pup would lick and chew (sometimes quite energetically) on another animal's ear. This was especially common when the potential partner happened to be asleep. Other times, a pup would nzzzle at another's rear flank. This latter behavior was of particular interest because a very similar pattern later occurred in the context of aggression.

Sometime between 26 and 30 days of age I noted a new method being used to elicit play; the "flip elicit" (described in Figure 14), which may have developed out of the stand-up paw. This motor pattern was used frequently to start play after about day 30, although there were still instances of eliciting via nuzzling at the rear flank.

The onset of flip-eliciting was related to a change in some of the other play behaviors, especially those loosely grouped under the term "wrestling." The "mutual bite" was an early form of wrestling; in older pups this became more of a "pin" in which one pup would stand over its partner and seem to keep him pinned down (Figure 13b). Perhaps the pin is an early display of dominance.

Finally, in even older pups (35 to 40 days +) the pin became more of a posture termed a "wrestle-head." This latter motor pattern was particularly common after a flip-elicit; one pup would be stretched out on its back while the partner was crouched over its head at a 90° angle (Figure 13c). In a supine variant of the head-wrestle, the two pups would be lying on their sides, but rather than being face to face, as in the prone-paw, one animal would curl itself around the other's head.

There appeared to be no special motor pattern used in terminating a play bout, although some behaviors were more common near the end of a bout than others. Generally, one of the partners would move away from the other, or they might stay in physical proximity, but engage in another activity. Self-grooming was particularly common after play.

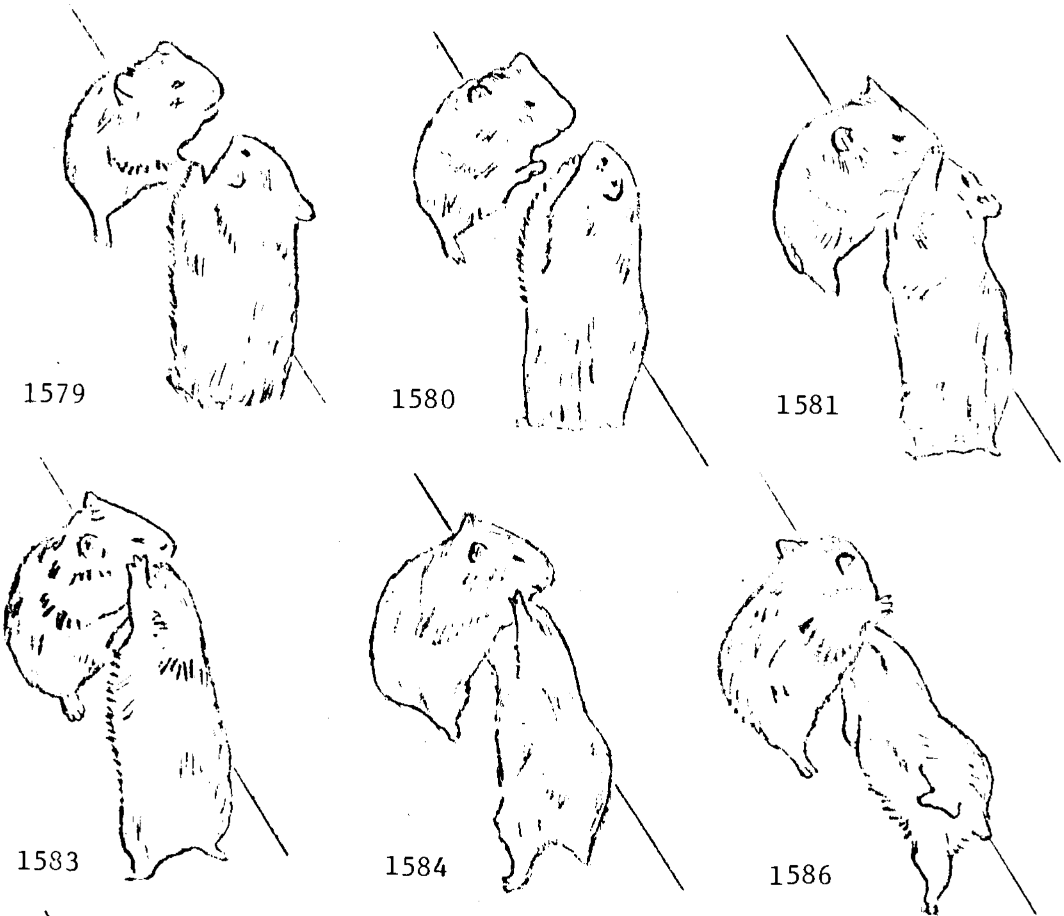


Figure 14. "Flip-elicit" in 33 day old pups. Traced from 16 mm movie film, shot at 16 frames per second.

Frames 1579,1580: The pup on the lower right approaches and raises left forepaw.

Frames 1581,1583: The eliciting pup can be seen to stretch forward and start to turn over, pushing with the rear paws.

Frames 1584,1586,1589: The pup completes the turn over onto its back. This particular "flip-elicit" did result in a play bout.

A summary of the ontogeny of motor pattern sequences in play is given in Figure 15. It can be seen that in general, as the pups got older (1) more motor patterns were involved in a play bout and (2) the sequencing of patterns (as shown by the arrows) became somewhat more complex. Fox and Clark (1971) found a similar increase in the number and variability of agonistic behavior sequences with age in the coyote (Canis latrans). They noted that the tendency towards increasing complexity is typical in the development of behaviors.

Motor Patterns in Aggression

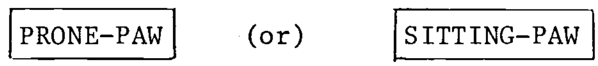
After the pups had reached 40 days of age, their play tended to appear more and more "serious." Vocalization, which had decreased considerably after day 25, and remained at a low level from days 30 through 40, began to increase again. I had often described play during the period of few vocalizations as "low-key"; now it was becoming more energetic. Although there were still a few bouts (particularly between two males) which were completely playful even on the last day of observations, after day 40 aggressive behavior took up an increasing proportion of the animals' time.

As mentioned above, female pups were the only ones to initiate outright aggressive encounters. A typical attack sequence would be as follows:

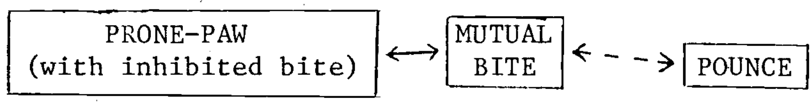
(1) A female pup would rush forward at another pup (the "lunge").

Figure 15. The ontogeny of motor pattern sequences in play. Dashed arrows represent an infrequent motor pattern sequence; a double arrow indicates an especially frequent one.

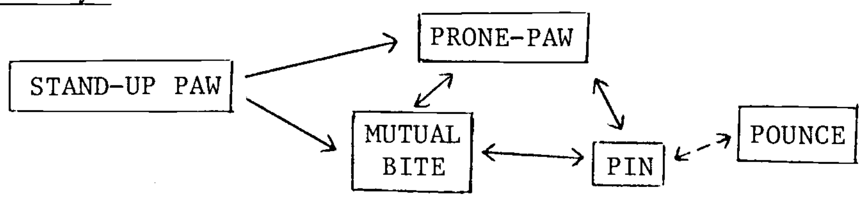
14 to 16 day old pups



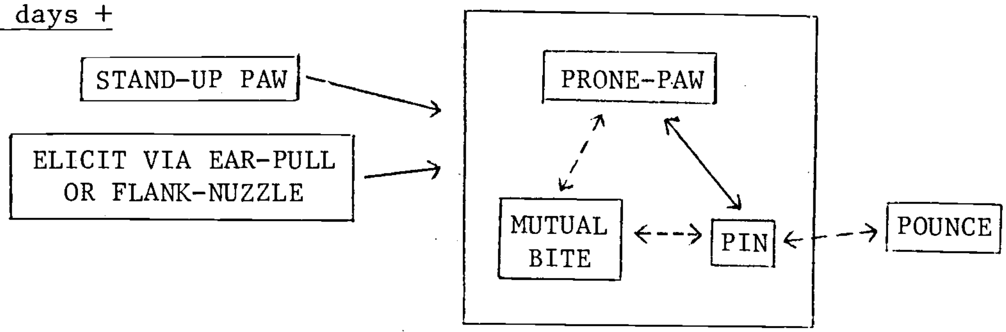
17 to 19 days



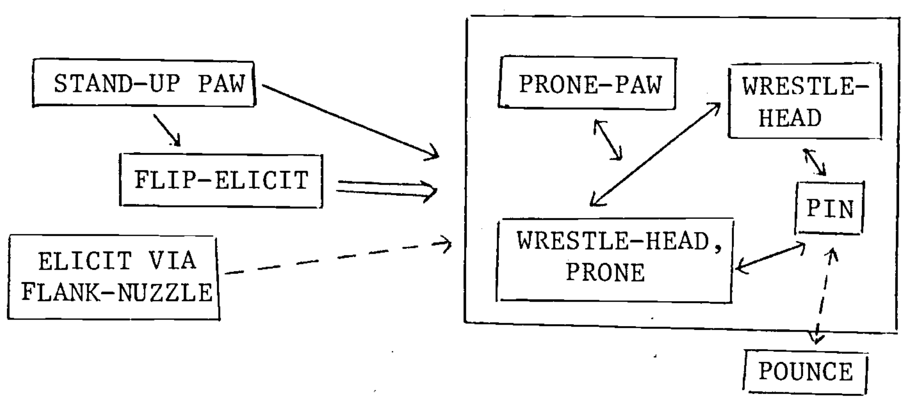
20 to 25 days



22 days +



26-30 days +



(2) Twisting slightly over, the attacking animal would nip at the rear flank area of the victim, and actually appear to be reaching underneath the other pup (see Figure 16). The twisting motion was reminiscent of that used in a flip-elicit.

(3) The attacked animal would attempt to run from its assailant, and the latter would give chase, usually amid loud vocalizations.

The above sequence was fairly stereotyped, and this type of aggressive encounter was termed a "lunge-attack." It was usually quite brief, lasting only a second or two.

In another, less common form of aggression, two animals would be engaged in what might look like a wrestling playfight; suddenly the wrestling would become vigorous, with shrill vocalizations coming from the pair. Finally, one animal would break away and run, with the other (always a female) giving chase. The chase differentiated such an encounter from what would have been termed a play bout.

Pups under attack often adopted what appeared to be "submissive" postures (Figure 17a). During an attack, the subordinate pup might be bowled over onto its back; it would remain there for a few seconds, all four paws in the air, and with a facial expression which seemed to indicate fear.

When not under direct attack, a pup might move away from an aggressive female, and sit up on the hind paws, the forepaws held in front. Grant and Mackintosh (1963) have termed this the "upright defense posture."

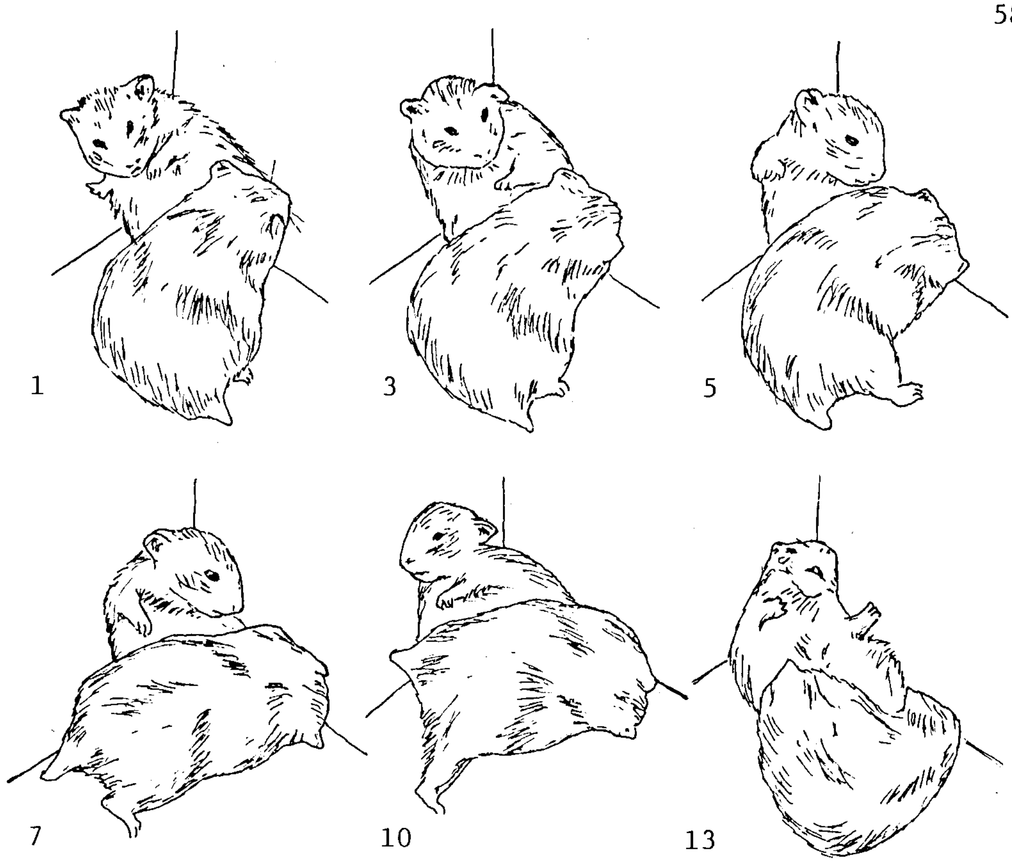


Figure 16. Attack sequence (49 day old pups). Traced from 16 mm movie film, shot at 16 frames per second.

Frame 1: A female (the lower animal) has approached another pup, who raises his forepaws in the upright defense position.

Frames 3,..,10: The aggressing pup starts to twist over onto her back, pushing with the hind paws.

Frame 13: She bites at the rear flank area of the victim, who is also flipped onto his back.

This sequence would often be followed by a chase.

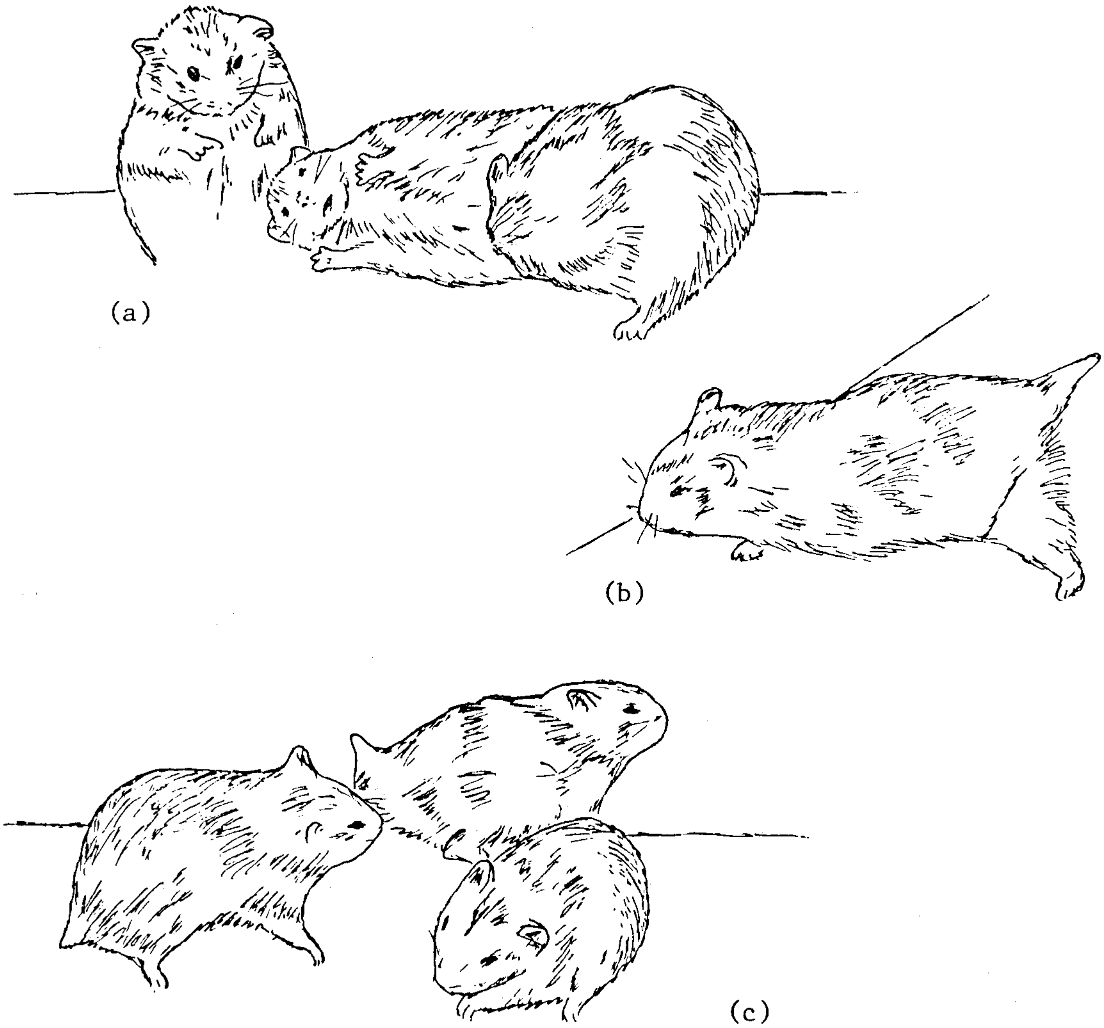


Figure 17. Submissive and sexual postures in the hamster.

(a). (48 day old pups) The middle pup is in the prone submissive posture, and is under attack by the female pup on the right. At the far left is a pup showing the upright defense posture.

(b). Female in lordosis.

(c). (49 day old pups) A chase, with the pup on the upper right showing the "tail-up" submissive posture. Note similarity to lordosis, including the flattened ears.

Traced from 35 mm slides and 16 mm movie film.

In a third type of submissive posture, a pup being chased would adopt a "tail-up" position while running away; this was similar to the lordosis position seen in estrous females (Figures 17b and 17c).

An edited movie film (approximately 150 feet at 16 frames per second) of hamster play and aggression is available from Dr. Dennis McDonald, Department of General Science, Oregon State University. It contains footage from the various rolls of film shot during this study.

DISCUSSION

The immediate result of this study was a large amount of detailed information concerning the structure of play behavior in golden hamsters; how much they played, for how long, and what it looked like. In the context of the structuralist-functionalist dichotomy, this would be the former approach.

Data on the form and appearance of play, and especially of how it changes as the animal develops, were seen to be needed in a wide variety of species. Yet it might be guessed that most ethologists are functionalists at heart, and the question of ultimate interest will always be -- <u>why</u> play?

The study was not aimed at testing any one theory of function. Nevertheless, the data obtained could be used to examine the applicability of certain hypotheses about play. The particular questions examined in the following discussion are:

(1) Is exercise the primary purpose of play?

(2) Does play aid in the establishment of positive social bonds?

(3) What is the relationship between play and agonistic behavior?

Berlyne's (1969) warning might be kept in mind: the function of play is probably not the same for all species, and even play in one species may have more than one function.

Play and the Muscle Exercise Hypothesis

Fagen and George (1976) stated that physical exercise is the simplest and physiologically most meaningful function for animal play. The idea dates back at least to Brownlee (1954), who felt that play in domestic cattle maintained tone and adequate vascularization in certain muscles. Fagen and George tested this muscle exercise hypothesis in pony foals and found that most exercise did occur during the play. They concluded that exercise was an important function of play.

Fagen and Young (in press, referenced by McDonald, 1977) then suggested that a further test of the hypothesis could be made by plotting the duration of play bouts as a survivorship function (as in my Results). If a convex curve resulted, it would be evidence that a primary function of play is exercise.

Basic to this approach is the assumption that muscles need to be exerted to near fatigue for best maintenance of strength and endurance (Astrand and Rodahl, 1970). If play serves primarily as a vehicle for exercise, most bouts should last long enough to cause the necessary fatigue. Thus one would expect an initial plateau on a survivorship curve (indicating few showt bouts) followed by a drop-off as the bouts reached the required length.

When McDonald plotted his data on bout duration (species: the California ground squirrel) as a survivorship function, the results looked similar to mine; the line was definitely not convex.

He therefore found no evidence to support the muscle exercise hypothesis in this species.

My results showed survivorship curves that were actually somewhat concave rather than convex, suggesting that exercise is not an important function of play in the hamster either. However, the slope of the plots did change with the age of the animals. It was considerably less steep for 30-33-day-old pups than for younger and older animals; the smaller slope indicating, on the average, longer bouts. If it could be shown that the development of muscles in young hamsters is timed so that 30-33-day-old animals have a special need for physical exertion, this would be better support for the muscle exercise hypothesis.

Without such evidence, I conclude that my results do not favor the idea that physical exercise is the primary function of play in hamsters (although it could well be a beneficial by-product). Subjective impressions from observing the pups support this conclusion. Some bouts were described in my notes as "vigorous," but others were termed "lazy," consisting mainly of a sequence of postures which seemed to require no more effort than grooming or walking around the cage.

Of course, because this hypothesis fails as an adequate explanation for play in the golden hamster does not mean that the conclusions of Fagen, George, and Brownlee are somehow less valid. The structure of play in the species with which they worked (horses and domestic cattle) is very different (involving such actions as galloping and "head-butting") and such large animals might well have a greater need for physical exertion to maintain muscle strength.

Play and the Development of Positive Social Bonds

An individual animal must presumably be able to recognize members of its own species and distinguish members of the opposite sex. The animal must know, or learn how to mate; when it lives as part of a group, the bonds that hold the group together must also be formed.

As mentioned earlier, the theory that play functions to develop these social skills currently has strong support. Yet even in primates the evidence has not been unequivocal. The classic work on rhesus monkeys by Harlow (e.g., Harlow and Harlow, 1962) had indicated that play contact among juvenile peers was essential for normal development of peer relationships and sexual behavior. However, a similar study by Meier (1965) seemed to show that play was _not_ necessary. Baldwin and Baldwin (1974) also found that many aspects of socialization (including group stability and mating) could develop normally in squirrel monkeys without social play.

More to the point are two studies of play in rodents. Wilson (1973) found that play in young voles (_Microtus agrestis_) helped maintain the cohesiveness of the family group; male voles with more play experience as juveniles were less aggressive towards new-born young.

Poole and Fish (1975), however, could find no evidence that play affected socialization in laboratory rats (*Rattus norvegicus*) and mice (*Mus musculus*). Both species have essentially the same social structure as adults, yet rats engage in a fair amount of social play, whereas mice do not.

The dearth of material on the social structure of adult golden hamsters in the wild makes it more difficult to evaluate the socializing role of play in this species. But my observations show that: (1) play is unlikely to be a mechanism for learning sexual behavior, and (2) play does not seem to aid in the establishment of social bonds which would lead to group stability.

The evidence for (1) is fairly clearcut. Whereas mounting is seen during play bouts in many other species (e.g., in primates (Dolhinow and Bishop, 1970); dogs (Bekoff, 1974b); meerkats (Wemmer and Fleming, 1974); the Columbian ground squirrel (Steiner, 1971); and the California ground squirrel (McDonald, personal communication)) it was never observed during play in hamsters. There were instances of mis-oriented and incomplete mounting, but these occurred only when a female was actually in estrus. Play mounting was not seen by Poole and Fish (1975) in their study of play in rats and mice, either.

The establishment of a cohesive social group was unlikely to be a function of play in hamsters from the start, as it is known that they are a highly aggressive species in the lab (Payne and Swanson, 1970, 1971) with females generally tolerating the presence of males only when in estrus (Floody and Pfaff, 1974).

Moreover, an extensive study by Eible-Eibesfeldt on the common hamster (Cricetus cricetus, closely related in behavior to M. auratus) had shown this animal to lead a solitary life. "Even in dense populations they defend their burrows and never form tribe-like groups" (Eible-Eibesfeldt, 1953).

Observation of my animals supported this: play did not lead to the establishment of a stable social group; instead fighting increased dramatically, and by the time observations ended (day 54) the litter was in a constant state of tension.

It is still possible that hamsters may learn species identity and the gender of other individuals through play. Dieterlen (1959), however, deprived some of his animals of social experience from a very young age, and reported that a hamster recognizes a conspecific and its sex by unlearned olfactory responses.

Play as the Ontogeny of Agonistic Behavior

It was not clear at the start of this study that play in young hamsters was closely connected to any particular adult behavior. Hours of observations, and repeated viewing of films led, however, to the suggestion that play bears a special relationship to later agonistic interactions.

The general possibility had not gone unremarked in the literature. Eible-Eibesfeldt (1975) had stated: "Animals that fight with members of their own species as adults practice the actions during playfighting." Several other authors had also emphasized this relationship (Fox and Clark; 1971; Steiner, 1971).

Poole and Fish (1975) found that two-thirds of social play in laboratory rats took the form of play-fighting. They therefore felt that social play was mostly playful aggression, and that this was true in many other mammals as well. Poole (1966) also found that almost all play in polecats was aggressive play. He stated that patterns of aggressive behavior in the adult polecat first appeared during play.

Evidence from my results in favor of a close relationship between play and agonistic behavior in hamsters includes:

(1) As play decreased after day 40, aggression increased.

(2) Vocalizations occurred in play and in aggression, but only rarely at any other time.

(3) Gender preferences were shown in both play and aggression. Although the nature of the preferences was not completely clear from my results, a further study concentrating on this one point is certainly feasible.

Stronger support comes from a consideration of the motor patterns in playful and agonistic encounters, as in many cases these patterns were similar.

The flip-elicit, for example, employed the same twisting motion that females later used in initiating an attack (compare Figures 14 and 16). Wrestling was seen in both play and aggression, and as the animals got older, the wrestling changed form. Mutual-bite gave way to the pin, and eventually to the wrestle-head, where one of the partners was stretched out flat on his back. In older animals, this latter posture was indicative of submission in agonistic encounters.

Figure 18, showing the sequence of behaviors in agonistic encounters, was taken directly from an article by Floody and Pfaff (1974) on aggression in female hamsters. Note that the "upright" posture is similar to stand-up paw, and the "on-back" position is equivalent to wrestle-head. The "rolling fight" seems to be a very aggressive version of mutual-bite. The sequence as a whole is markedly similar to the patterns seen in play. The main exception is the addition of flight behaviors at the end of an agonistic interaction.

The play behaviors that were indicative of dominant-submissive relationships are particularly interesting because one might expect to see the establishment of a dominance hierarchy as part of the development of agonistic behavior.

Dolhinow and Bishop (1970) have noted that the amount of physical contact in play enables individuals to learn the strength and speed of their play partners: "The total experience makes ranking possible and seemingly inevitable."

As mentioned above, later forms of wrestling in hamster play seemed to include more dominant/submissive elements than earlier forms. In addition, the pups vocalized more during early play; by the time patterns such as flip-elicit and wrestle-head were seen, vocalizations had decreased substantially.

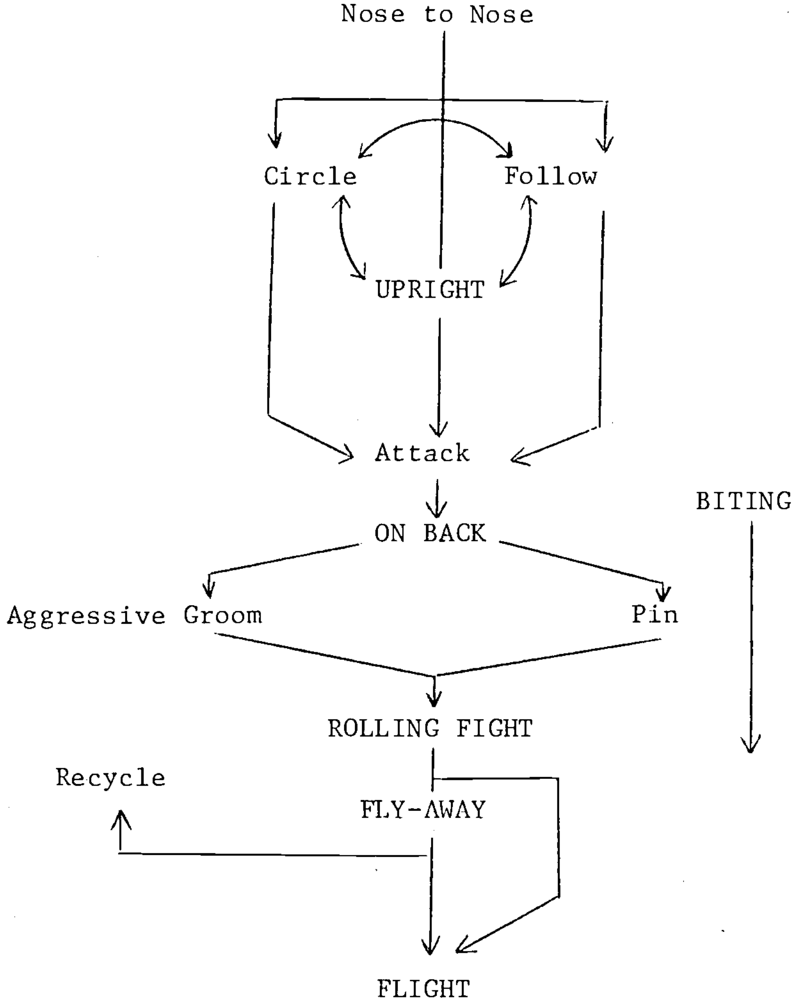


Figure 18. Sequence of behaviors in agonistic encounters between female hamsters. Taken from Floody and Pfaff (1974). Their description of some of the behaviors are given below:

UPRIGHT: "...an individual has neither forepaw in contact with the substrate, and is within 1 body length of her opponent."

ON BACK: "...a situation in which an individual is lying on its back or side...with its opponent typically in an upright posture, oriented at a right angle to and hovering over the supine individual."

ROLLING FIGHT: a "pattern of violent aggressive behavior... Typically, the bodies of the two antagonists are perpendicular to, and wrapped tightly around each other, their abdomens in close apposition."

Perhaps a dominance hierarchy was forming during earlier interactions; in the later bouts the establishment of this hierarchy resulted in less antagonism between pups. Some support for this idea comes from my observations; the particularly aggressive females ("bullies") were clearly dominant over the other animals from the first day attacks were observed (around days 35-40).

It is interesting to note that Fox and Clark (1971) had seen a similar pattern of development in the coyote: interactions between pups were somewhat aggressive until about a month of age, when fights apparently established a dominance hierarchy. After the fights, encounters became more playful.

If we accept that play in golden hamsters may bear a close relationship to later agonistic behavior, the next question would be, what is the nature of this relationship?

There are at least two possible ways of approaching the answer. One way, widely employed in the literature, is to say that play is practice for aggression. Another tack would be to call play the ontogeny of aggression.

There may be no testable difference between the two approaches, yet the difference in connotation is substantial. "Practicing" seems to mean that the animal needs to *learn* how to be aggressive, and could not perform agonistic behaviors correctly as an adult without juvenile play experience. It may also imply that hamster pups know they will need to improve skills for later life, an idea I reject.

I suggest that in this species play is better described as the ontogeny of aggression. The animal has certain instincts causing the onset of play. As it grows, intrinsic maturational processes result in changes in the structure of play, until a point is reached where the complete sequence of agonistic behaviors can occur.

What might the intrinsic maturational processes be? Numerous studies on the hamster (see Floody and Pfaff (1974) for a review) have shown that aggression is connected with the presence of certain gonadal hormones. Since estrous females were first seen in my litters at approximately the same time that play began to decrease (and agonistic encounters increased) it may be that the shift from play to aggression is linked to sexual maturity. Methods to test this hypothesis would presumably be straighforward, involving the removal of gonads and various replacement therapies in young animals.

A final question remains. If play in hamsters is the ontogeny of aggression, are we justified in continuing to call it play? Certainly it has many of the characteristics said to define this behavior (more common in the juvenile animal, apparently without immediate purpose), yet something seems lacking when it is compared, for example, to play in a pet dog.

The entire subject is fraught with semantic confusion and an irresistible tendency towards anthropomorphism (e.g., Loizos'

(1966) statement that "animals do not work and therefore cannot be said to play"). It is suggested that at this stage in our understanding it would be best to concentrate on the details of play, or play-like behaviors, leaving semantic discussion to a later date.

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APPENDIX

The method used to calculate the expected frequencies given in Table 6 was as follows:

Consider a litter of seven hamsters with f females and m males.

$$\text{Total number of pairs} = \binom{7}{2} = 21$$

$$\text{Number of mixed pairs} = f \cdot m$$

$$\text{Number of female/female pairs} = \binom{f}{2}$$

$$\text{Number of male/male pairs} = \binom{m}{2}$$

Suppose we have n independent selections from the population of pairs. Each selection corresponds to a play bout. If we let

P_X = the probability of a mixed pair

P_F = the probability of a female/female pair

P_M = the probability of a male/male pair

we then have the following expected probabilities after allowing for the various sex ratios in different litters:

	f=5,m=2	f=4,m=3	f=2,m=5
P_X	10/21	12/21	10/21
P_F	10/21	6/21	1/21
P_M	1/21	3/21	10/21

If we then observe

N_X = the number of mixed pairs

N_F = the number of female/female pairs

N_M = the number of male/male pairs

our chi-square statistic for the i-th litter (i = 1,..,4) is

$$\chi_i^2 = (N_X - nP_X)^2/nP_X + (N_F - nP_F)^2/nP_F + (N_M - nP_M)^2/nP_M$$

with 2 degrees of freedom. With four independent litters we can also form

$$\chi^2 = \chi_1^2 + \cdots + \chi_4^2$$

with 8 degrees of freedom as our test statistic.

Similar reasoning is used to calculate the expected values in Table 8 (number of female/male attacks versus number of female/female attacks). In this case, however, the total number of pairs is limited because a female is always involved; as the initiator of an attack she is considered the first member of every pair. The total number of possible pairs is then:

the number of female/male pairs, or $f \cdot m/2$

plus

the number of female/female pairs, or $\binom{f}{2}$.

If we now let

P_{FM} = the probability of a female attacking a male

P_{FF} = the probability of a female attacking a female

we can then obtain the following expected probabilities for each litter:

	f=5,m=2	f=4,m=3	f=2,m=5
P_{FM}	1/3	1/2	5/6
P_{FF}	2/3	1/2	1/6

Chi-square is calculated as above, but with only one degree of freedom.

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