

Eliciting Play: A Comparative Study

(*Octodon*, *Octodontomys*, *Pediolagus*,
Phoca, *Choeropsis*, *Ailuropoda*)

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SYNOPSIS. The social play behavior of six mammalian species (Rodentia, Pinnipedia, Artiodactyla, Carnivora) is described and compared. Locomotor and Rotational Movements, e.g., jumping, running, and headshaking, occurred in all species and predominated in the rodent play. These movements are similar in form to anti-predator and "protective" responses and result in an immediate but temporary cessation of sensory stimulation from conspecifics.

Investigation of body odors was the most important stimulus eliciting Locomotor-Rotational Movements in the rodents. In the larger mammals, body odor sniffing was enhanced during play, but specialized signals from other sensory modalities elicited and maintained play interactions. The possible functions of a heightened exchange of olfactory information during juvenile social development are discussed.

INTRODUCTION

In this paper, we will emphasize some characteristics of play which have been previously overlooked, by describing and comparing the social play of six unrelated and diverse species of mammals.

First, we will demonstrate that a group of behavior patterns, which we have termed Locomotor-Rotational Movements, is com-

mon to the social play of several species. These behavior patterns include head shaking, body twisting, jumping, and running, and are considered to be play because they are exaggerated forms of normal locomotor and rotational body movements found in other functional contexts, such as anti-predator behavior. The exaggerated quality arises from an increase both in the amplitude of the movement (e.g., height jumped or distance covered during a leap) and the rapidity of execution of the movement. Also, the different Locomotor-Rotational Movements are variously combined and occur simultaneously and animals repeatedly return to the stimulus source, thus distinguishing the activity within family groups (i.e., "play") from behavior involving movement away from a noxious or dangerous stimulus. In Table 8 there is a comparison of the occurrence of these behavior patterns in the six species of our study.

Since Locomotor-Rotational Movements may occur when an individual is alone, this type of play has often been considered "spontaneous" (Müller-Schwarze, 1971). However, we will show that sniffing conspecifics, or perceiving olfactory stimuli arising from conspecifics in the absence of a conspecific results in these movements being

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performed immediately. Seeing a conspecific jump, run, or head-shake also results in the performance of Locomotor-Rotational Movements.

The majority of species we observed also displayed interactive play which has been discussed more commonly in the play literature (see Poole, 1966; Ewer, 1968; Loizos, 1969; Rasa, 1971; Horwich, 1972; Wilson, 1974a).

We have divided social play into two major categories, Companion-Oriented and Solo Play. In Companion-Oriented Play, there is contact (at least sniffing contact) between two animals, regardless of whether both individuals participate equally in the interaction. Typically, we use the terms mutual and/or dyadic interaction to refer to social play with participation by both animals. Solo Play is defined as the performance of Locomotor-Rotational Movements in the absence of tactile contact with a conspecific. Since perception of conspecific odor or visual stimulation from conspecific may elicit Locomotor-Rotational Movements in a lone animal, Solo Play, as we have defined it, is distinguishable from Solitary or Object-Oriented Play where there is no input from or orientation towards a conspecific.

Throughout this paper, we have paid special attention to the association between olfactory investigation and play behavior. This association has been overlooked or excluded by other authors (e.g., Bekoff, 1972). The dependence of locomotor play on ol-

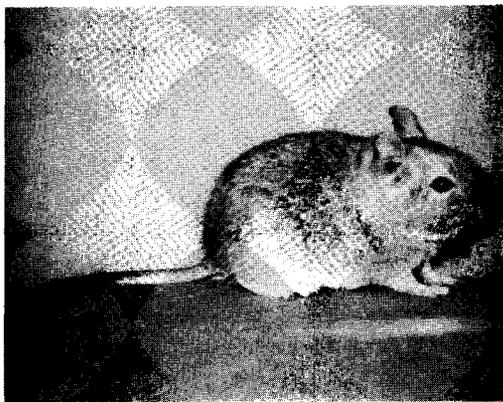


FIG. 1. *Octodon degus*.

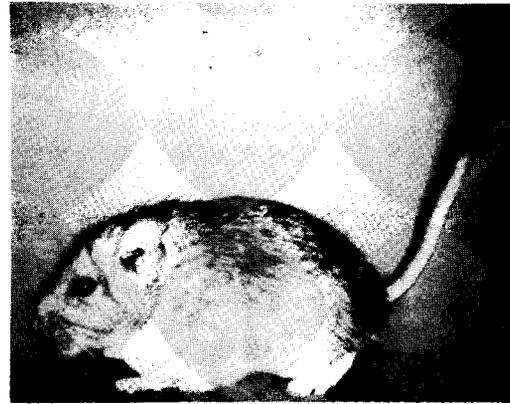


FIG. 2. *Octodontomys gliroides*.

factory investigation has also been shown for a myomorph rodent, the vole, *Microtus agrestis* (Wilson, 1973). We will present some evidence to support our hypothesis that olfactory exchange is enhanced during play. Behavior here termed "play" is defined in the appendices.

Our approach emphasizes an analysis of context. Thus, we are concentrating on stimulus-response relationships and will not discuss motivation in a broad sense (but see Meyer-Holzappel, 1956; Loizos, 1967; Müller-Schwarze and Müller-Schwarze, 1969).

THE CAVIOMORPH RODENTS: *Octodon degus*,

Octodontomys gliroides, AND *Pediolagus salinicola*

Animals

Observations have been made on family groups in captivity of three South American caviomorph rodents: the degu, *Octodon degus*, the choz-choz, *Octodontomys gliroides* (both Family Octodontidae), and the salt desert cavy or dwarf mara, *Dolichotis (Pediolagus)*¹ *salinicola* (Family Caviidae) (see Fig. 1, 2, 3).

These animals are so little known that an outline of their general form and natural history may be useful to an understanding of their play (see also Table 1).

Octodon degus, one of the three species of *Octodon*, is found in Peru and Chile, living in burrows in grassy places between the coastal region and the mountain foothills (M. Schamberger, personal com-

¹ Referred to throughout as *Pediolagus*.



FIG. 3. *Pediolagus salinicola* (sandbathing).

munication; Walker, 1964). *Octodontomys gliroides*, a monotypic species, comes from the altiplano of Bolivia and Chile and lives in burrows among rocks, shrubs, and cacti (Walker, 1964). *Pediolagus salinicola* is found in the salt plains of northern Argentina (Cabrera, 1953), where it shelters in thin scrub, venturing cautiously out into the exposed grassland to feed (Smythe, 1970).

All three species live in family groups in captivity. Field observations of *Pediolagus* (Smythe, 1970) and *Octodon* (G. Fulk, personal communication) confirm that this is the natural condition. *Octodontomys* is less known, but has not been observed in such aggregations (Schamberger, personal communication; Rowlands, 1974). Quite probably the male *Octodontomys* is not bound to the same burrow as the female.

Anatomically, *Octodon* and *Octodontomys* are

TABLE 1. Main characteristics of ecology, social organization, and behavior of *Pediolagus salinicola*, *Octodon degus*, and *Octodontomys gliroides* (Caviomorpha).

Habitat	<i>Octodon</i>	<i>Octodontomys</i>	<i>Pediolagus</i>
	Temperate or subtropical savanna or scrub	Semi-arid montane scrub	Temperate steppe
Mode of life	Terrestrial/fossorial	Terrestrial/fossorial	Terrestrial
Activity	Diurnal	Nocturnal	Diurnal
Social organization	Colonial; extended family groups; possible pair bonding between parents	Pair and immediate offspring; adult male permanently cohabiting with female?	Pair and immediate offspring
Social behaviors not in play context:			
Enurinating (by male)	+	+	--
Allogrooming	+++	++	--
Huddling (one on top of other)	+++	+	--
Behaviors related to olfactory and tactile exchange which may be involved in play:			
Sniffing another animal	+++	+++	+
Sandbathing	+	++	+++
Urinating	++	++	+++
Play behaviors:			
Locomotor-Rotational Movements	+	+++	+++
Solo play	+	++	+++
Companion-Oriented play	+++	+++	+
Mutual Upright, Supine-Quadrupedal and other mutual dyadic interactions	+++	+++	--
Father participates in play	--	++	+
Mother participates in play	--	+	+

typically rodent in form (adult weights about 250 to 350 g and 150 to 250 g respectively), whereas *Pediolagus* resembles a long-legged hare (estimated adult weight about 2 to 3 kg) (Figs. 1, 2, 3).

Both *Octodon* and *Octodontomys* have tails about as long as the head and body, with a brush of black hairs at the tip, more pronounced in *Octodontomys* than in *Octodon*. *Octodontomys* pelage is gray along the dorsum and pure white along the ventrum, and is soft to the touch. *Octodon* fur is more bristly, being brown along the dorsum and creamy-white along the ventrum. *Octodontomys* eyes are much larger than *Octodon*'s, indicating its crepuscular or nocturnal habits (Rowlands, 1974), whereas *Octodon* seems to be mainly diurnal (Fulk, personal communication). *Pediolagus* has brown/gray fur which is only slightly paler on the underside, and has a very short tail. It seems to be mainly diurnal.

The young of all three species are precocial. *Pediolagus* litters consist of one or two young (birth weight about 250 g), which resemble the adult but in miniature. Within a few minutes of birth, the young can not only walk and run, but also sandbathe in a coordinated fashion. They nurse for about a month, although they also feed on solids from birth. Maternal care is limited to nursing and ano-genital grooming. Our eldest juvenile female first conceived at about 4 months. Play occurs from the day of birth.

Octodon and *Octodontomys* are less developed at birth, although the eyes are open and they are furred (weights about 11 to 13 g and 18 to 21 g respectively), and their locomotion is uncoordinated. Feeding on solid food appears on the second or third day, as do the first elements of play. Play develops rapidly during the second week, when sandbathing also appears. The young nurse for about 5 weeks. Perforation of the vaginal closure membrane, indicating puberty, has been observed in *Octodon* at about 45 days and in *Octodontomys* at about 3 to 4 months.

Methods

Family groups of the three species have been observed routinely in their home enclosures. The enclosures provide ample space for vigorous activity (100 X 65 X 45 cm for *Octodon* and *Octodontomys*; 420 X 200 cm for *Pediolagus*). They contain nest boxes, logs, and gnawing blocks and either a large pan containing sand placed on a substrate of woodshavings, or a wholly sandy substrate. The sand is usually saturated by body odors and urine since all three species sandbathe and urinate in the sand. The animals are fed rat chow, nuts, seeds, fresh fruit, and vegetables.

For each species, observations were made at a time when group activity was expected. All animals were on a 12-hr light/12-hr dark cycle. *Octodontomys* was observed under red light immediately after the lights went out. *Octodon* was observed at intervals while the lights were on, and *Pediolagus* was ob-

served shortly before the lights went off, after the animals had been fed. Most of the observations were tape-recorded and later transcribed. To date, nine litters of *Octodon*, five of *Octodontomys*, and two of *Pediolagus* have been followed. This paper will include only some of these observations.

A summary of the social activity and play patterns observed in family groups²

During activity periods in *Octodon* and *Pediolagus*, bouts of social interactions and play regularly alternated with other functional categories of behavior, such as feeding. By contrast, in *Octodontomys* family groups, the onset of activity was followed by a long period of uninterrupted social interactions which was only later followed by feeding.

Social interactions among family members during activity periods involved mainly approach and naso-body contact, followed by withdrawal. Sandbathing (Fig. 3), urination, and occasional enurination (not observed in *Pediolagus*) complemented naso-body contact in comprising much of the socially oriented behavior within undisturbed family groups (Table 1) (but see Kleiman, 1974, for a description of social behavior in other contexts, e.g., courtship).

An increase in the frequency of these behaviors (except for enurination) was correlated with an increase in the frequency of occurrence of Locomotor-Rotational Movements. A detailed analysis of the context in which these movements occur and their relative frequencies among the three species can be found below.

During heightened activity, behavior patterns involving prolonged body contact between two animals were seen in *Octodon* and *Octodontomys* but were absent in *Pediolagus* (Table 1).

One pattern, the Mutual Upright or bipedal interaction, has been described in rodents in an agonistic context (e.g., Clarke, 1956; Eisenberg, 1962, 1963a, 1967; Grant and Mackintosh, 1963; Barnett, 1963). When it occurs in sibling juvenile rodents

² Play patterns and associated activities of the three species of caviomorph rodents are described in detail in Appendix 1.

coupled with a relaxed body tone, the Mutual Upright has been termed "play fighting" (e.g., Müller-Schwarze, 1971). We will use the term Mutual Upright in order to avoid commitment to a specific motivational interpretation.

The Mutual Upright with incisor-interlocking occurs in *Octodontomys* play and has also been described for the heteromyid rodents (the Locked Upright) in a fighting context (Eisenberg, 1963a). During the Supine-Quadrupedal interaction, the supine and quadrupedal animals of the dyad display postures similar to those which have been interpreted as submissive and dominant respectively in several myomorph rodent species (e.g., Clarke, 1956; Eisenberg, 1962; Grant and Mackintosh, 1963). Thus, some *Octodon* and *Octodontomys* play patterns resemble behavior seen during agonistic interactions in other rodents.

Another dyadic interaction occurring as part of social play was Riding. The components of supporting the forelegs and forebody on the partner's back (or sitting on the mother's back) and prolonged nosing of the nape (*Octodontomys* young) or riding another animal while nosing its nape (*Octodon*; see Fig. 8Bh) are similar to pre-huddling behavior, except that during play the animals are moving. It is also similar to mating behavior, except that during sexual mounting by adult male *Octodon* and *Octodontomys* (and also mounting of juveniles by *Octodon* fathers) the nape is not nosed (Kleiman and Wilson, unpublished). In both the acouchi, *Myoprocta pratti*, and the domestic guinea pig, also, the nape is nosed during "sexual" behavior of juvenile males, but not of adult males (Kunkel and Kunkel, 1964; Kleiman, 1971). Nape nosing does, however, occur as a prelude to the male's mount in some myomorph rodents (reviewed by Ewer, 1968).

From Table 1 and the above description, it is clear that in *Octodon* and *Octodontomys*, Companion-Oriented Play, i.e., play with body contact, was more frequent than Solo Play, whereas the reverse was true of *Pediolagus*, i.e., in *Pediolagus*, dyadic interactions rarely occurred.

Sandbathing behavior was common to all

three species. Members of *Octodontomys* families frequently all sandbathed at the same locus, often one after the other. The tendency to overlap sites was less marked in *Octodon* and individuals did not sandbathe in turn. In *Pediolagus*, family members sometimes sandbathed in turn; unfortunately we cannot comment on the degree of locus-specificity since our *Pediolagus* family group was only provided with a single sand pan.

Eisenberg (1963b, 1967), in an analysis of the sandbathing behavior of several species of myomorph rodents, found preferences for particular sites and noted that during encounters overlap of individual sandbathing loci occurred, particularly in the less communal species. This conclusion supports our own impression that *Octodontomys* is less social than the highly communal *Octodon*.

Sandbathing sites are an important source of olfactory stimuli originating from conspecifics (Eisenberg, 1963b, 1967). In *Pediolagus* and *Octodontomys*, Locomotor-Rotational Movements occurred at sandbathing sites and following urination and sandbathing by individuals. The temporal association between olfactory stimulation and Locomotor-Rotational Movements will be discussed below.

The level of participation by parents in play activities differed between the three caviomorph rodent species. *Octodon* parents did not display Locomotor-Rotational Movements nor participate in dyadic play interactions with their offspring. *Octodontomys* parents displayed Locomotor-Rotational Movements during Companion-Oriented Play but did not exhibit Solo Play. They also participated extensively in dyadic interactions with offspring. In *Pediolagus*, both parents and young displayed Locomotor-Rotational Movements, but mainly in the context of Solo Play.

The occurrence of Locomotor-Rotational Movements

In *Octodon*, *Octodontomys*, and *Pediolagus*, six different movements were distinguished in the category Locomotor-Rota-

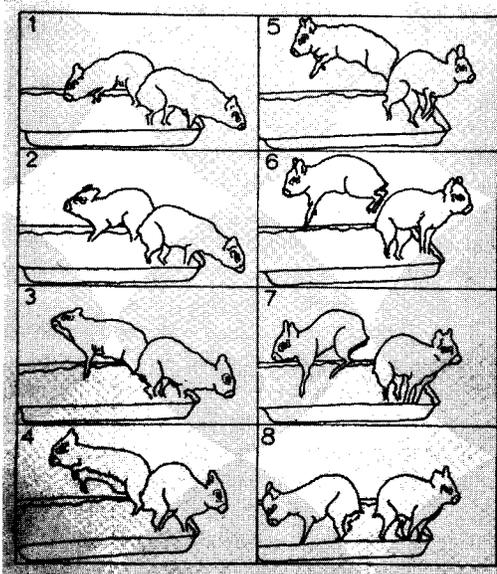


FIG. 4. A play jump by subadult *Pediolagus* (♀ on left; ♂ on right). 1, The female sniffs the substrate; 2, raises her head; 3, gives a small head toss; and 4-8, leaps. Simultaneously (4-8) the male gives a smaller leap, the left hind leg remaining on the ground (0.36 sec from 1-8).

tional Movements. These are described in Appendix 1. One group comprised Locomotor Movements and included the jump (Fig. 4), turn (Fig. 5), hind-leg kick-back, and running, while the other group, Rotational Movements of the body, included head shakes, head tosses, and body twists. Although we have separated these two groups of movements, individual movements may occur in combination, such as a jump with a head shake.

The relative frequency of occurrence of the six Locomotor-Rotational Movements differed according to the social context in *Octodon* and *Octodontomys*. Rotational Movements were relatively more common during Companion-Oriented play than during Solo play, whereas Locomotor Movements were relatively more common during Solo play than during play involving a partner (Table 2). Furthermore, within Companion-Oriented play, head shakes immediately followed sniffing another animal most often, jumping next often, and running least often (Table 3).

In *Pediolagus*, few Locomotor-Rotational Movements occurred after sniffing another animal (Table 4). In general, Locomotor Movements predominated, as was found in *Octodon* and *Octodontomys* Solo Play (Table 2). Rotational Movements occurred in *Pediolagus* after sniffing another animal, sandbathing (by the actor), sniffing the substrate or standing close to a sandbathing conspecific relatively more often than did Locomotor Movements (Table 4).

In all three species, sniffing the body odor of a group member was most likely to result in head-shaking or body twisting, less likely to result in jumping, and least likely to result in running. In all three species, running occurred much less often than jumping and head-shaking.

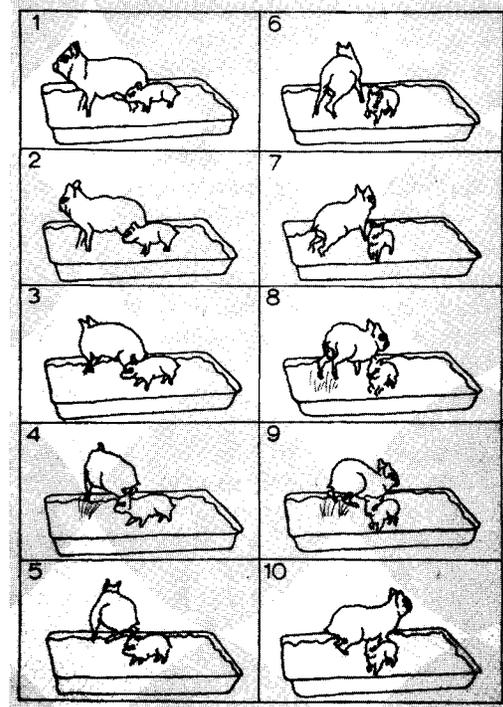


FIG. 5. A play jump with turn by a subadult ♀ *Pediolagus* (week old young on right). 2-4, Head turn resulting in a 90° shift of orientation; 5-6, jump, bringing the rest of the body through a 90° turn from the starting position; 7, fore quarters turn through a further 90°; 8-10, jump, bringing the rest of the body through a second 90° turn; 10, the animal finishes facing in the opposite direction from the start (0.39 sec from 1-10).

TABLE 2. A comparison of frequency of occurrence of Locomotor-Rotational Movements displayed by the young of three rodent species (given as per cent of total observed Locomotor-Rotational Movements [n]).

Species and Litter No.	Rotation Movements		Locomotor Movements				Total (n)
	Headshake %	Body twist %	Jump %	Turn %	Run %	Kick-back %	
<i>Octodontomys</i>							
Young with mother							
IV	56	2	36	5	1	0	86
V	49	11	31	3	5	0	140
Young with father							
IV	61	6	28	1	4	0	69
Young with young							
V	45	7	34	8	6	0	332
Solo							
IV	13	3	51	23	10	0	39
V	17	6	40	19	18	1	126
<i>Octodon</i>							
Young with young							
VII	46	10	35	0	9	0	191
Solo							
VII	0	0	77	0	23	0	13
<i>Pediolagus</i>							
Young in all contexts							
II	22	11	43	12	9	3	705

TABLE 3. Locomotor-Rotational Movements by young *Octodon* and *Octodontomys* which followed sniffing another animal (per cent of total occurrence of that movement in the context listed).^{a,b}

Species and Litter No.	Rotation Movements		Locomotor Movements		
	Headshake (n)	Bodytwist (n)	Jump (n)	Turn (n)	Run (n)
<i>Octodontomys</i>					
Litter II ^c					
Young sniffs mother		95 (25)		72 (18)	(4)
Young sniffs father		93 (43)		83 (19)	(7)
Young sniffs young		80 (94)		72 (91)	20 (20)
Litter IV					
Young sniffs mother	90 (48)		71 (31)	(4)	(1)
Young sniffs father	100 (42)	(4)	53 (19)	(1)	(3)
Litter V					
Young sniffs mother	87 (69)	81 (16)	77 (44)	(4)	(7)
Young sniffs young	91 (145)	69 (19)	61 (114)	50 (28)	30 (20)
<i>Octodon</i>					
Litter VII					
Young sniffs young	98 (88)	90 (20)	65 (66)	0 (0)	23 (17)

^a Note that two or more different movements may follow a sniff.

^b Where *n* was less than 10, a percentage was not calculated.

^c Head shake and body twist, and jump and turn are not separated in the analysis.

TABLE 4. Acts immediately preceding and following Locomotor-Rotational Movements by *Pediolagus* (behavior of entire family group).

Act following	Act preceding						Locomotor Movements	Rotational Movements	Total
	Sniff animal	Sand-bathe	Perineal drag	Sniff inanimate	Visual or tactile stimuli	Miscellaneous			
Sniff animal							23	13	36
Sand-bathe							23	19	42
Perineal drag							11	6	17
Sniff inanimate							24	13	37
Visual or tactile stimuli							114	48	162
Miscellaneous							75	47	122
Locomotor Movements	33	20	7	32	123	49	75	35	374
Rotational Movements	26	19	3	36	61	31	31	36	243
Total	59	39	10	68	184	80	376	217	1,033

The italic cells indicate significant linkages. The linkage was taken to be significant if the difference between the observed and expected values was greater than three times the square root of the expected value (McKinney, 1961).

Stimuli associated with Companion-Oriented and Solo Play

As we have seen in *Octodon*, play is almost exclusively Companion-Oriented; in *Octodontomys* there is some Solo Play, although Companion-Oriented Play predominates; and in *Pediolagus* only a small amount of play is Companion-Oriented, the remainder being Solo. Since Companion-Oriented Play involves sniffing specific areas of the companion's body, perception of individual odors must be enhanced during this type of play. By contrast, since Solo Play involves sniffing the sand at communal urinating and sandbathing sites, this type of play involves the perception of group odors. The reason for the different emphasis on Companion-Oriented and Solo Play in the three species is unclear at present. In this section the olfactory stimuli involved in both kinds of play will be evaluated. Then *Octodontomys* and *Pediolagus* will be contrasted from this point of view.

In *Octodon* and *Octodontomys*, play (as already discussed and described in Appendix I) involves frequent naso-body contact with a companion. In the *Octodontomys* families, where intense social activity was uninterrupted by prolonged bouts of feed-

ing, the total number of nosing contacts initiated by the young was proportional to the activity time (Fig. 6).

Nosing contacts were also proportional to the amount or "intensity" of play as measured by a "play intensity score" (see Appendix 2 for explanation of scoring method). In Litter I, the amount of play per nosing contact was greater between the two young (a male and a female) than between the young and mother (Fig. 7a,b).

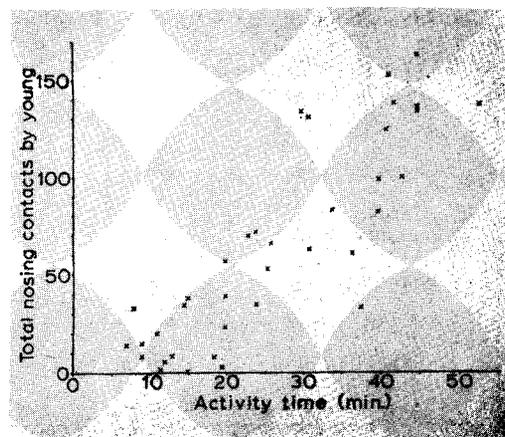


FIG. 6. The relationship between activity time and the number of nosing contacts initiated by the two young of an *Octodontomys* litter.

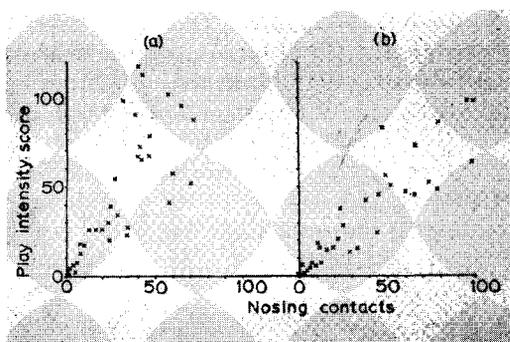


FIG. 7. The relationship between the number of nosing contacts and the amount of play ("play intensity" score) by the two young of an *Octodontomys* litter. *a*, behavior between the two young; and *b*, behavior between either of the young and the mother.

During ontogeny the intensity and amount of play in this litter increased together with, but more rapidly than, the frequency of nosing contacts up to 30 to 40 days, after which time both nosing contacts and play fell off slightly, play more so than nosing (Wilson, unpublished). This implies that the stimulatory effects of nosing another

animal may vary during ontogeny in this species.

Different parts of the body and different age and sex classes had different "potencies" for stimulating Locomotor-Rotational Movements on the part of the nosing animal. *Octodontomys* young generally displayed fewer Locomotor-Rotational Movements after nosing the mother than after nosing either the father or each other. Sniffing the nape and nose-mouth regions was more likely to result in Locomotor-Rotational Movements than was sniffing the rump and tail regions, although the mother's naso-mouth region was less stimulating than her nape (Table 5). Table 5 also gives an estimate of the total amount and "intensity" of play (via the "play intensity score") associated with the different body regions. As an example, the young displayed few Locomotor-Rotational Movements after nosing the father's tail, even though they frequently nibbled and pulled it.

There were considerable inter-family differences in the frequency of occurrence of

TABLE 5. The effect of sniffing different parts of the body on the occurrence of Locomotor-Rotational Movements and "play intensity" in *Octodontomys* (n = number of nosing contacts).

Context and Litter No.	Nose/mouth		Nape		Rump		Tail	
	I	II	I	II	I	II	I	II
	(n)		(n)		(n)		(n)	
Young sniffs mother								
II	9	0.49	14	0.41	3	—*	5	0.71
	(59)		(117)		(68)		(131)	
IV	8	0.97	22	0.45	31	—	15	0.96
	(74)		(129)		(35)		(76)	
V	11	0.85	26	0.67	12	—	17	1.14
	(117)		(163)		(41)		(190)	
Young sniffs father								
II	30	2.3	17	0.31	0	—	8	0.68
	(115)		(42)		(12)		(61)	
IV	24	1.56	38	0.76	11	—	0	0.87
	(81)		(63)		(35)		(23)	
Young sniffs young								
II	30	1.20	23	0.47	6	—	4	1.20
	(241)		(206)		(100)		(164)	
V	28	1.25	49	1.28	21	—	27	1.48
	(127)		(224)		(52)		(19)	

I = Per cent nosing contacts immediately followed by Locomotor-Rotational Movement by the sniffing animal.

II = Ratio of "play intensity" score to total number of nosing contacts (see Appendix 2 for explanation of "play intensity" score). ("Play intensity" score associated with naso-nose/mouth contact between young and a parent includes the behavior of the parent.)

*— = Not calculated.

Locomotor-Rotational Movements resulting from sniffing the different body regions. One major contributing factor to this may have been the different ages of the parents and numbers and sex of the young. It is possible that the skin of animals of different ages and sexes has different stimulus properties; this has not yet been investigated.

Whether or not this frequent naso-body contact among *Octodon* and *Octodontomys* family members can be distinguished from truly investigatory behavior was studied by comparing the observations with the investigatory behavior of unacquainted pairs of young in a strange environment (Wilson, unpublished). Neither Locomotor-Rotational Movements nor Mutual Upright interactions occurred between any unacquainted *Octodon* young in a strange enclosure ($n = 75$ 15-min encounters), but Locomotor-Rotational Movements did occur when unacquainted *Octodontomys* young investigated one another in the same situation ($n = 4$ 15-min encounters). Although the ratio with which different parts

of the body were nosed (generally nape $>$ nose/mouth $>$ rump) was indistinguishable in the two situations, in the unfamiliar enclosure none of the naso-nose/mouth contact occurred together with Mutual Upright or Supine-Quadrupedal interactions. However, the manner of nape- and rump-nosing in the unfamiliar enclosure was indistinguishable from that in the home environment.

From this comparison of the behavior in the family group and unfamiliar situations, therefore, it has not been possible to draw a clear distinction between investigation of strangers and the naso-body contact which results in Locomotor-Rotational Movements.

Pediolagus young displayed Locomotor-Rotational Movements after sniffing another animal less frequently than *Octodontomys* young (for example, see Table 6). Moreover in *Pediolagus* (Litter II), the percentage of Locomotor-Rotational Movements following sniffing the substrate or being in proximity to a sandbathing animal

TABLE 6. *Companion-Oriented and Solo Play in sand pan in Octodontomys Litter V and Pediolagus Litter II.*

Behavior	<i>Octodontomys</i> (2 ♀ ♀ young) (n)	<i>Pediolagus</i> (1 ♂ and 1 ♀ young) (n)
% occasions in sand in which Locomotor-Rotational Movements occurred	55 (125)	67 (186)
% total play bouts which occurred in sand pan	27 (336)	66 (268)
% sandbathing bouts which were followed by Locomotor-Rotational Movements	23 (65)	41 (76)
% of occurrence of sniffing sand or standing beside sandbathing animal which were followed by Locomotor-Rotational Movements ^a	25 (32)	29 (186)
% urinations or perineal drags followed by Locomotor-Rotational Movements	0 (4) ^b	29 (34)
% sniffing other animal followed by Locomotor-Rotational Movements	27 (990)	11 (364)

^a For the *Octodontomys* litter, this measure comprised only proximity to a sandbathing companion.

^b More urinations observed outside sand pan, none of which was followed by Locomotor-Rotational Movements.

was always greater than after sniffing another animal. This difference between the percentages increased from 6% of the total play bouts in week 1 ($n = 110$) to 13% in week 2 ($n = 91$) to 18% in week 3 ($n = 56$) and finally to 28% in weeks 4 to 5 ($n = 114$), although the percentage of Locomotor-Rotational Movements after sniffing another animal did not change (12, 10, 18, and 11% respectively). This indicates that sniffing the substrate or being close to a sandbathing conspecific (both in the area of the sand pan) became a progressively stronger stimulus for eliciting Locomotor-Rotational Movements as the *Pediolagus* young developed when compared with directly sniffing a conspecific.

In one *Octodontomys* family (Litter V), the extent to which the young oriented their activity towards the sand pan was compared directly with *Pediolagus* Litter II (Table 6). Fewer of the total bouts of Locomotor-Rotational Movements and dyadic play interactions occurred in the sand in *Octodontomys* when compared with *Pediolagus*. However, when the *Octodontomys* young did enter the sand pan, they displayed Locomotor-Rotational Movements almost as often as did the *Pediolagus* young, and when a companion sandbathed beside a youngster, the youngster exhibited Locomotor-Rotational Movements as often as did *Pediolagus* juveniles. However, an *Octodontomys* juvenile that sandbathed or urinated was less likely to follow with Locomotor-Rotational Movements than were *Pediolagus* young.

It was interesting that there was far more Solo Play in this litter (Litter V) than in four other *Octodontomys* litters observed on a wholly sandy substrate (e.g., compare frequencies of Solo Play in Litters IV and V in Table 2). Fifty-nine percent of the Solo Play bouts ($n = 68$), but only 20% of the Companion-Oriented Play bouts ($n = 268$), took place in the sand pan in Litter V. However, the presence of a companion in the sand clearly acted as a stimulant. When a single young entered the sand pan ($n = 62$), Solo Play occurred 42% of the time, whereas when one juvenile and the mother, both young, or both young and the

mother entered the sand pan together ($n = 28, 29, \text{ and } 6$ respectively), Companion-Oriented or Solo Play occurred 61%, 69%, and all of the time respectively.

A further detail concerns the amount of Locomotor-Rotational Movements by one of the young when standing beside a sandbathing animal. Although the mean figure for this was 25% of all possible sandbathing bouts (Table 6), on 7 of 14 occasions when the mother sandbathed beside an offspring, Locomotor-Rotational Movements were performed by that young. By contrast, only 1 of 18 sandbathing bouts by a young was followed by its sibling displaying Locomotor-Rotational Movements.

The sequencing of behavior during Companion-Oriented Play of Octodon and Octodontomys

Most interactive play of *Octodon* and *Octodontomys* consisted of bouts lasting several seconds, of the multiple nosing contact type with intermittent Mutual Upright and Supine-Quadrupedal interactions (see Appendix 1 for description). The sequencing during these play bouts has been analyzed for young-young play of *Octodontomys* Litters II and V and *Octodon* Litter VII by tabulating the behavioral sequences in contingency tables (see Appendix 3a, b, and c). Figure 8A,B shows the significant linkages (individuals of a dyad were identified only in the *Octodontomys* records) for *Octodontomys* Litter II and *Octodon* Litter VII.

Several general points emerge from this analysis that seem to characterize the nature of this kind of play.

1) Sequencing exists, but is not necessarily the same in different litters. Mutual Upright interactions were much less important to the play of Litter V than Litter II (*Octodontomys*), and in Litter V did not occur in any significant linkage. On the other hand, sandbathing occurred only occasionally in the play of Litter II (on a sandy substrate), but more often in the play of Litter V (where sand was concentrated in a pan and the substrate was wood shavings), when it was significantly linked to

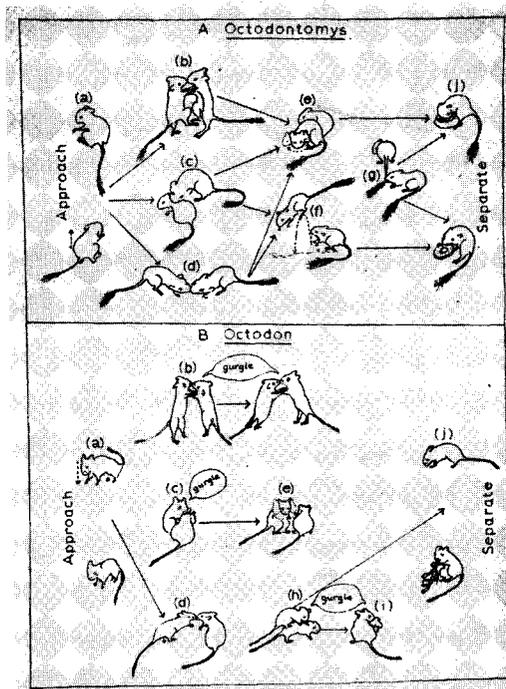


FIG. 8. Sequencing of *Octodon* and *Octodontomys* play. The arrows denote significant linkages calculated for *Octodontomys* Litter II and *Octodon* Litter VII. a, Approach; b, Mutual Upright interaction; c, nosing the companion's nape; d, naso-nose/mouth contact; e, headshaking by the partner that made naso-body contact; f, jump by the partner that made naso-body contact; g, tail nibbling/pulling; h, riding; i, circling with reciprocal nape nosing; j, separate.

approaching and play running by the other young. Naso-nose/mouth contact was followed significantly often by Locomotor-Rotational Movements in Litter II, but not in Litter V.

2) The sequence of behavior tends to go in one direction only, from approach to Mutual Upright or Supine-Quadrupedal interactions or multiple nosing contacts, to Locomotor-Rotational Movements and separation of the pair. This means that although, for instance, a Mutual Upright interaction with Locomotor-Rotational Movements may be followed by further nosing contacts with Locomotor-Rotational Movements, or vice versa, there is a strong tendency towards completion of the interaction, that is, separation of the pair.

3) Although in *Octodon* and *Octodontomys*, Locomotor-Rotational Movements do occur in the middle of a play bout, they tended to terminate ongoing dyadic activity. They apparently function to "cut off" olfactory input to the sniffing animal. However, analysis of *Octodon* Litter VII showed that 45% of headshakes ($n = 88$) and 100% of body twists ($n = 20$) were immediately followed by further nosing interaction, compared with only 13% of jumps ($n = 66$) and 6% of runs ($n = 17$). By contrast, 64% of jumps and 82% of runs, but only 35% of head shakes and 5% of body twists were followed by immediate separation. Therefore, Locomotor movements terminated dyadic activity much more predictably than did Rotational Body Movements.

4) In *Octodontomys* Locomotor-Rotational Movements by one animal were rarely followed immediately by Locomotor-Rotational Movements by the partner. In *Pediolagus* Litter II only 9% of Locomotor-Rotational Movements ($n = 403$) occurred immediately after Locomotor-Rotational Movements by a group member. (This was lumped with other "visual and tactile stimuli" in Table 4.)

5) An act by one animal tended to be followed by another act by the same animal, although the active member of a dyad did sometimes change. Thus, play bouts tended to be one-sided except in the case of mutual/dyadic activities (such as Mutual Upright interactions). This was particularly true of Litter V, which only seldom engaged in mutual/dyadic activities.

THE HARBOR SEAL, *Phoca vitulina concolor*

Methods

An isolated population of this subspecies of the common (harbor) seal, *Phoca vitulina*, was observed on Sable Island, Nova Scotia, during the pupping season, between May 15 and June 19, 1973. For a description of this herd during the pupping season, see Boulva (1971).

One herd consisting largely of adolescents hauled out along the sandy shoreline between 0500 and 0700 hours and returned again to the water about 1600 to 1800 hours. Play occurred predictably between 0530 and 0730 hours, taking place in the shallow water of the breaker zone and on the wet

sand at the water's edge. Mothers with pups adhered less strongly to this haul-out rhythm and were active in the shallows at any time during the day. The occurrence of play between mother and pup was therefore unpredictable.

Observations were tape-recorded and later transcribed, incorporating a time check at 15-sec intervals, which was the basis for the quantitative analysis. Only relatively prolonged play bouts (more than 5 min) were used in this analysis. For mother-young play, 14 play bouts (mean duration = 17 min) were used; for adolescent play, 12 bouts (mean duration = 16 min).

Only some of the play patterns are considered here. A summary of all the play patterns observed is given in Appendix 4.

Play soliciting

One animal would begin a play bout by leaning its chin or head and shoulders over its partner's body (Fig. 9). The body tone of the soliciting animal was noticeably relaxed. This relaxed body tone was characteristic of all the seal behavior defined here as "play." This behavior was repeated continually, particularly when play took place at the water's edge. It was interpreted as "play soliciting" by analogy with the same behavior seen in the grey seal, *Halichoerus grypus*, where both animals had to repeat the posture continually for play to proceed (Wilson, 1974a). Reciprocation of this signal in the Sable Island harbor seal often occurred, but did not seem to be critical provided the partner responded positively in another way. This behavior was also

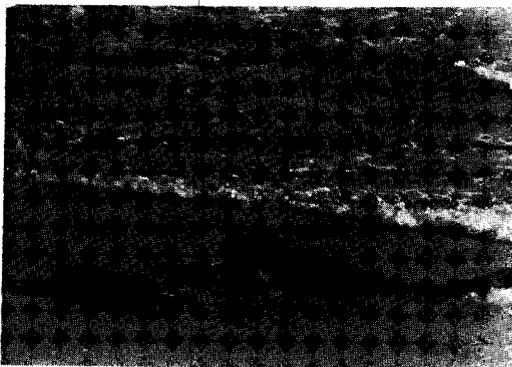


FIG. 9. An adolescent harbor seal, *Phoca vitulina concolor*, gives the play-soliciting signal to a companion by leaning its head and shoulders over the other's body.

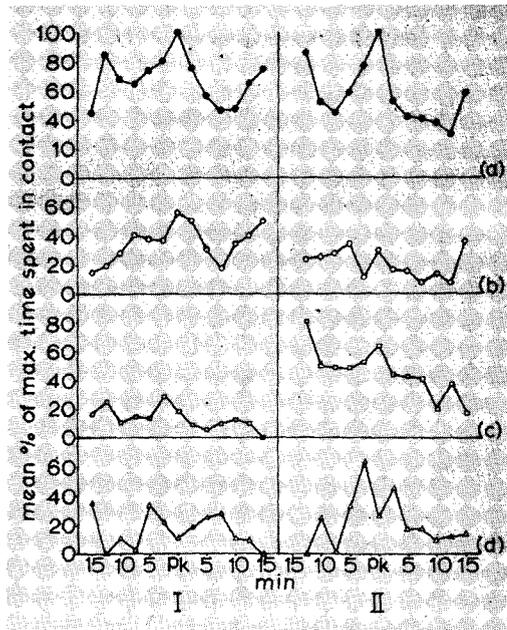


FIG. 10. The temporal patterning of play by the harbor seal, *P. v. concolor*. I, Adolescent play ($n = 9$ play bouts). II, Mother-pup play ($n = 10$ play bouts). a, Total body contact; b, Head-Over-Back "play-soliciting" signal; c, naso-body contact; d, Locomotor-Rotational Movement. Pk: 100% body contact (reference point).

seen twice by a mother towards her pup outside a play context, immediately after snapping at the pup. It was also observed by adult males as a prelude to sexual mounting of females on the beach, particularly when the females protested.

The patterning of play

Each play bout was quite distinct in character, since the different play patterns occurred in different relative proportions, regardless of whether play took place on the beach or in the water (Wilson, unpublished). The individualistic quality of the bouts was in marked contrast to the uniformity seen in the aquatic play of juvenile *P. v. vitulina* (Wilson, 1974a). Despite this, there was a correlation in the waxing and waning of several components of behavior, including total body contact, the Head-Over-Back "play-soliciting" signal, naso-body contact, and Locomotor-Rota-

tional Movements (see Appendix 4 for description of the very varied Locomotor-Rotational Movements).

To demonstrate their relationships, the 2½-min interval in which mutual body contact was highest (per cent of ten 15-sec intervals) in each play bout was taken as a reference point, and the average amount of contact for each 2½-min interval preceding and following this peak was calculated as a percentage of the peak. The average amounts of the play components were then plotted in the same way with respect to the reference, or highest, point of contact. Thus, we could control for the fact that the peak period of body contact occurred at different times during the course of a play bout (see Fig. 10).

In adolescent play the amount of Head-Over-Back soliciting was fairly well correlated with the total amount of contact, whereas this relation was not obvious for mother-pup play (Fig. 10*b*). By contrast, naso-body contact only roughly follows the total contact curve in adolescent play, whereas these measures are well correlated in mother-pup play. However, Head-Over-Back soliciting was more common in adolescents than in mothers and pups, while the reverse condition was true for naso-body contact (Fig. 10*b,c*). Locomotor-Rotational Movements were negatively correlated with total contact in adolescent play, with no clear relation for mothers and pups.

In Figure 11, the positive relationship between the frequency of naso-body contacts and the frequency of the Head-Over-Back

signal can be seen. The ratio of the frequency of naso-body contacts over the frequency of the Head-Over-Back signal was significantly higher in mother-pup play than in adolescent play ($P < 0.004$, Median test).

In adolescent play, naso-body contact occurred significantly more frequently in the water than on the beach, whereas the Head-Over-Back signal occurred more frequently on the beach than in the water. These tendencies were also detected for mother-pup play, but were not statistically significant (Wilson, unpublished). This difference between mother-pup and adolescent dyads may account for the difference seen in Figure 10*b,c* and Figure 11.

From these analyses it is clear that, despite the individualistic quality of play bouts, there was a waxing and waning of close contact which seemed to correspond to the waxing and waning of the Head-Over-Back play-soliciting signal in adolescents, but to naso-body contact in mothers and pups. Possibly the inequality in the size of mother and pup was related to the lower frequency of Head-Over-Back signals.

Naso-body contacts

During play different parts of the body were nosed selectively, as shown in Figure 12. The regions around the muzzle and the nape received most attention, the trunk, hind flipper, anus, and genital regions very little. Observations on mother-pup interactions in other contexts (Wilson, unpublished) have indicated that the parts of the body most often nosed during play are also the focus of attention in other functional contexts. The pup's neck region was most often sniffed by the mother when there seemed to be some confusion of identity (Fig. 13). Abandoned pups sometimes sucked one another, and this sucking was most often directed at the neck region. When a pup followed its mother in the water, it always oriented towards the nape and nosed the nape intermittently as it caught up with her. The mother's response was usually to stretch the head back, whereupon the pup nosed her between the eyes. Fol-

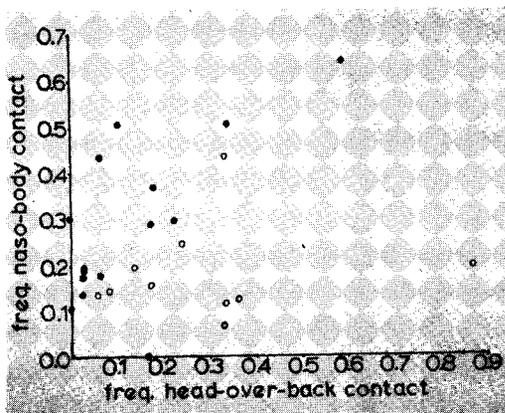


FIG. 11. The relationship between the frequency of the Head-Over-Back "play-soliciting" signal and the frequency of naso-body contact during play of the harbor seal, *P. v. concolor*. ○ = adolescent; ● = mother and pup.

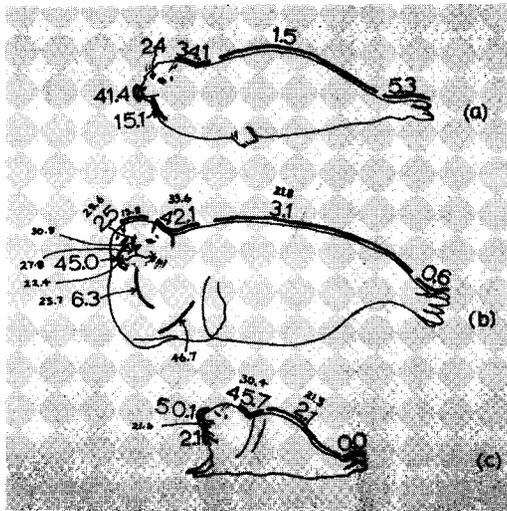


FIG. 12. The relative importance of nosing different parts of the body during play of the harbor seal, *P. v. concolor*. Large figures indicate the percentage of the total nosing contacts directed at the body regions indicated. The line along the back refers to any part of the body between the foreflippers and the tail. *a*, Adolescent ($n = 205$ nosing contacts); *b*, pup noses mother ($n = 157$); *c*, mother noses pup ($n = 140$). (Note: In calculating the % of naso-nose/mouth nosing of *b* and *c*, a half of the total naso-nose contact was attributed to each animal. Observations supported this assumption.) Small figures indicate the relative amounts of sebaceous material surrounding the hair follicles (mean for all hair follicles counted) divided by the mean number of hairs per follicle seen in the same section. *b*, Pregnant female close to parturition. *c*, Abandoned female neonate.

lowing this, the pup sometimes nosed the mother's muzzle, whereupon she might turn around, bringing the pair into direct muzzle-to-muzzle contact. Both patterns were also shown by the mother to the pup, especially following a brief separation.

Another context in which the nape was involved was in sand-rubbing. After the morning haul-out and just before returning to the water in the evening, the seals often lie on their backs in the wet sand near the water's edge and vigorously rub their necks and shoulders on the sand at a locus corresponding to their resting site. Mothers frequently back-rubbed during the day as they returned to the beach with their pups after a swim.

On the beach the pup often nosed its

mother's chest between the fore-flippers, sometimes as it began to search for the nipples, although the chest was seldom nosed during play.

All these observations suggested that the skin is producing odoriferous substances, particularly in the muzzle and neck regions. To the human nose, the neck region had a strong, musky odor, while the angle of the jaw had a qualitatively different, much stronger odor.

To investigate this hypothesis, skin samples were taken from one dead pregnant female (due to give birth) and from three abandoned pups. The skin was sectioned so that the hair follicles were cut in transverse section, and the amount of sebaceous gland material surrounding the follicles was counted.

A preliminary estimate of the amount of sebaceous material present in the skin of different parts of the body (based on the pregnant female and a female pup) (Fig. 12) indicated that the neck region has more glandular material than the muzzle, which has more than the trunk. The top of the nose and the region between the snout and the upper lip in the adult had slightly more material than the angle of the jaw and nearly as much as the nape, suggesting that odor perception may play a significant role in muzzle-to-muzzle contacts, in addition to the tactile sensations resulting from vibrissae contact. The fact that the regions between the eyes and between the foreflippers (especially the latter) appear to have a lot of sebaceous material, but are nosed primarily in non-play contexts, sug-



FIG. 13. A mother harbor seal, *Phoca vitulina concolor*, about to sniff her pup's neck.

gests that the quality of the odor may be different in these regions. Also, the small quantity of material on the top of the head (from between the eyes to the nape) suggests that the scent secreting areas may be localized. Although these results may be modified after the examination of additional animals and body regions, at present they indicate that odor "input" is increased during social interactions and especially play, by the naso-body contacts. They also suggest the nosing animal may choose to sniff different body areas in different functional contexts and thus "control" the quality and quantity of olfactory input.

THE PYGMY HIPPOPOTAMUS,
Choeropsis liberiensis.

Methods

A mother and female calf pygmy hippopotamus were observed in their home enclosure at the National Zoological Park. In the early afternoons, when all observations were made, the animals were confined to an elongate area containing a pool of water with concrete steps at one end. The depth of the water in the pool increased along with the calf's development. The pair were observed ($n = 29$ half-hour periods) when the calf was between 16 and 84 days old. Observations were written directly. (For a description of enclosures and husbandry, see Stroman and Slaughter, 1972.)

Companion-Oriented Play between mother and calf

The behavior observed consisted of the following components: (a) body-to-body contact, (b) mother pushing the calf in front of her, (c) naso-body contact, (d) chin and cheek rubbing, (e) defecating, (f) sniffing and chewing feces and sniffing the steps, (g) muzzle-to-muzzle contact, (h) Locomotor-Rotational Movements, (i) water agitating (splashing), (j) lying with head or head and body on side, (k) gaping, and (l) jaw nibbling. These components are described in detail in Appendix 5.

Components (a) to (f) were not specific to play (called non-play). Components (g) to (l) were considered play activities. Water agitating (i), lying on the side (j), and gaping (k) were included here because of the

quality of movement or body tone (see Appendix 5). These components were performed mostly by the mother and had the appearance of play soliciting behavior owing to the mother's orientation to the calf, who was often not playing at that time, and to the calf's frequent positive response (see Appendix 6). Muzzle-to-muzzle contact was considered a play activity only after an analysis of the contexts in which it occurred (see below).

The behavior components which were not specific to play nevertheless tended to be concentrated in time around the play activities.

This was investigated by (i) considering ongoing behavior as occurring in sequential 5-min periods; (ii) dividing all 5-min periods into those in which a play activity (h-1) occurs at least once and those in which no activity specific to play occurs; (iii) tabulating the number of times all components of behavior occurred in both categories; and (iv) expressing these numbers as totals for each category over all observations.

Table 7 shows the per cent occurrence of the non-play components during the 5-min periods which included at least one play activity.

Only defecation (e) by the mother did not increase in frequency during play. However, sniffing and chewing feces (f) did occur more often in play periods than at other times. Muzzle-to-muzzle contact (g) occurred almost exclusively during the 5-min play periods (92% occurrence, $n = 53$), which was why it was considered a play activity.

The play activities interpreted as play soliciting (water agitating, approaching partner while lying on the side, gaping) and also Locomotor-Rotational Movements may provide visual stimuli to the other animal and also proprioceptive stimuli to the actor. By contrast, the non-play activities may provide mainly olfactory and tactile stimulation. To see whether or not the non-play activities could have been acting as eliciting stimuli for the play activities, or vice versa, the behavior was considered as a two-act sequence (Appendix 6). The only linkages that differed significantly from expectation were muzzle-to-muzzle contact resulting in one animal gaping, gaping (usually by the mother) re-

TABLE 7. The occurrence of non-play components during play in the pygmy hippopotamus, *Choeropsis liberiensis*.

Component	Total observed occurrence	% occurrence during 5-min play period
(a) body contact	191	66
(b) mother pushing calf	52	62
(c) naso-body contact	185	70
(d) chin and cheek rubbing	30	63
(e) defecating	100	54
(f) sniffing and chewing feces, and sniffing substrate	54	72

Play occurred in 78/173 (45%) of the 5-min observation periods.

sulting in the calf jaw-nibbling, and defecating by the mother resulting in the calf sniffing and chewing her feces. This suggests that the non-play activities did not immediately precede play, and vice versa. Grouping the acts into play and non-play confirmed that play acts tended to be followed by further play acts rather than by non-play acts (194:157) and non-play acts tended to be followed by further non-play acts rather than by play acts (211:141) (Chi-squared = 16.1; $P < 0.001$).

The conclusion, therefore, is that the heightened activity during play leads to an increased level of tactile contacts as well as olfactory exchange behaviors (naso-body contact, cheek/chin rubbing, and sniffing of maternal odors by the calf).

THE GIANT PANDA, *Ailuropoda melanoleuca*.

Methods

A pair of juvenile giant pandas, *Ailuropoda melanoleuca*, was observed outdoors in adjoining enclosures which provided visual, olfactory, and auditory but not tactile contact. Observations on social behavior were conducted mainly in the early morning between June 1972 and March 1973, but additional data on other aspects of behavior were collected at all hours of the day indoors, where only olfactory and auditory contacts were permitted. Play behavior directed towards the partner was seen outdoors, and compared with play directed towards inanimate objects under both housing conditions.

Behavior was recorded on tape and later transcribed to check-sheets divided into 5-sec intervals. Behavior frequencies were computed by summing the number of 5-sec intervals during which a particular pattern occurred, and expressing it as a percentage of the total.

For the purposes of this paper, approximately 9 hr of outdoor observations have been analyzed,

which included 51 play bouts by the male and 44 bouts by the female ranging in duration from 30 sec (the minimum duration arbitrarily defined as a play bout) to 10 min, 30 sec and averaging 2 min, 35 sec for the male and 2 min, 5 sec for the female. The play was analyzed by considering what preceded the initiation of a bout by a single individual, and what effect, if any, a play bout by one panda had on the partner. The occurrence of specific play patterns in different contexts, e.g., after approaching or sniffing the partner was also examined.

The natural history of the giant panda and a summary of captive maintenance and behavior can be found in Morris and Morris (1966), Collins and Page (1973), and Perry (1973).

Companion-Oriented Play between two juveniles

Companion-Oriented Play patterns in the giant panda are readily identifiable as play due to the quality of the movement and the absence of such patterns from most other functional contexts. One series of movements involves Rolling usually by somersaulting (Fig. 14) or rolling laterally



FIG. 14. Somersaulting during play in the giant panda, *Ailuropoda melanoleuca*.

while lying on the ground. These patterns may occur several times in succession. Lateral rolls and somersaults may not be fully executed, resulting in the panda's either lying on the ground on its back or venter or halting while in a head-under, partly curled-up posture. A vertical surface may be used for support, and this results in such postures as the leg cock, supported headstands and handstands (reversed upright) as well as movements such as cartwheels. This series of postures forms a transitional sequence. Only the leg cock and handstand are observed in another functional context, i.e., scent-marking involving urination and anogenital rubbing by the male (Kleiman and Collins, 1972).

While lying on the back or sitting upright, the panda may writhe or curl up; in these positions, the forepaws are often used to hold, pull, and otherwise manipulate the hind limbs and the tail, and various parts of the body may be mouthed. Locomotor-Rotational Movements seen during social play include running to and from the partner, head tossing, head shaking, and body twisting.

Play behavior directed towards a partner may be interspersed with object-oriented play; when toys, such as basketballs, plastic hoops, and metal kegs, were available, these were incorporated into the activity in 46% ($n = 51$) of male and 31% ($n = 35$) of female play bouts. The behavior towards the toys included, in addition to previously described patterns, butting with the nose and swatting with a forepaw. Such behaviors could not be exhibited towards the partner since tactile contact was prevented, but during a series of introductions indoors when the female was thought to be in estrus, paw swatting was prevalent and the rolling behavior was reduced in frequency.

Because the pandas were denied physical contact, certain behaviors were seen during social interactions which suggested "frustration" and "thwarting." Both animals would bite at the wire fence dividing their enclosures and the female especially would dig at the gravel next to the fence. Moreover, the type of play observed was clearly affected by the housing procedures since

during the introductions (as mentioned above), the quality of the interaction altered considerably (although no mating occurred). However, the housing conditions probably allowed us to observe considerably more "play-soliciting" behavior than would have been possible had the animals been living together on a daily basis.

The major group of behavior patterns which we considered to be solicitation signals were those involving rolling movements. Although somersaults and lateral rolls occurred throughout a play bout, they often occurred as the first behavior pattern. Sixty-two percent of male and 75% of female social play bouts were begun with a somersault, completed lateral roll, or roll over onto the back. In fact, the rolling often accompanied an approach to the partner, e.g., the male would be separated from the female and would display uninterrupted multiple lateral rolls during his approach to her.

Behavior patterns accompanying or following all approaches to the partner, in both play and non-play contexts, consisted of rolls, sniffing, following, withdrawing, etc. When the male approached the female, a rolling movement occurred 43% of the time ($n = 63$), while when the female approached, she rolled 58% of the time ($n = 69$).

A further finding which supported the suggestion that rolling movements were

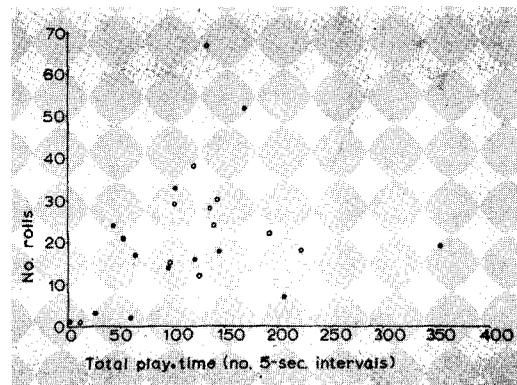


FIG. 15. The relationship between the number of rolling movements and the length of play bouts in the giant panda, *Ailuropoda melanoleuca*. ● = male; ○ = female.

play solicitation signals was that the number of rolls during an observation session was closely correlated with the total play time during that watch, but only up to a point. Figure 15 demonstrates this relationship separately for the male and female, and suggests that in long play sessions relatively less rolling is seen.

The effectiveness of rolling movements, as such, in inducing a play response from the partner was not established. However, the response of each panda to a play bout (including rolling movements, but also the other behavior patterns mentioned above) by the partner was analyzed. For the male, 46% ($n = 50$) and for the female, 73% ($n = 44$) of all play bouts began when the partner was already playing. Of male play bouts alone ($n = 27$), 30% resulted in the female's joining in within 30 sec and 56% during the course of that bout. The male was even more likely to respond to the female's play than vice versa. Of 12 bouts initiated by the female, the male joined in within 30 sec on 8 occasions and on 11 of 12 occasions responded by playing before the female had completed her bout. Thus, play by one panda clearly induced a play response by the partner.

Despite the fact that tactile contact was prevented, some attention was paid to what an individual did after sniffing the partner through the fence. For the male, 55% of

the sniffs ($n = 29$) were followed immediately by a Rotational or other play pattern (head shaking, rolling, headstand, handstand, etc.), and 76% by a play pattern within 30 sec. Similarly, the female exhibited a play pattern within 30 sec after a sniff 60% of the time ($n = 20$). This suggests that sniffing the partner may be involved in eliciting play in the giant panda, although rolling movements and other play patterns, which are visual stimuli, elicit play more often.

DISCUSSION

Locomotor-Rotational Movements

Locomotor-Rotational Movements occurred during the play of all six species (see Table 8) and were a major component of the entire play repertoire in *Pediolagus*, *Octodon*, and *Octodontomys*. Similar behavior has been described by other authors (e.g., African ground squirrels, *Xerus erythropus*, Ewer, 1966; three species of caviés, Rood, 1972; warhogs, *Phacochoerus aethiopicus*, Frädrieh, 1965). In the rhesus monkey, *Macaca mulatta*, analysis of movement has revealed not a discrete headshake, but rotation of the head and shoulders together with abduction of the limbs. This postural component is unique to play (Sade, 1973).

The diversity of species which display

TABLE 8. *Locomotor-Rotational Movements* (parentheses denote occasional occurrence).

	Rotational movements	Locomotor movements
Rodentia		
<i>Octodon</i>	Head shake, body twist	Jump, run
<i>Octodontomys</i>	Head shake, body twist	Jump, turn, (hind-leg kick-back), run
<i>Pediolagus</i>	Head shake, head-toss, body twist	Jump, turn, hind-leg kick-back, run
Pinnipedia		
<i>Phoca</i>	Head shake, head toss, head and foreflipper waving, body "wiggling" and "thrashing," (rolling on own axis in air)	Rearing and "high diving," leaping, "torpedoing," "whooshing," "hovercrafting," (all aquatic), bouncing (terrestrial)
Artiodactyla		
<i>Choeropsis</i>	Head shake, head toss, stretching head up, body undulating, (corkscrew action of head)	Leaping, (pirouetting on hind legs) (aquatic)
Carnivora		
<i>Ailuropoda</i>	Head shake, head toss, body twist	Running

these movements suggests that they may be ubiquitous to mammalian play, whether or not they are a major component of the play repertoire.

The Locomotor Movements appear to be related to anti-predator behaviors (Müller-Schwarze, 1971; Kleiman, 1974). Morris (1962) suggested this connection by referring to *açouchi* play as "play" or "vacuum fleeing." Ewer (1966) also suggested a link between the "jinking" of ground squirrels and true escape behavior.

In *Phoca*, the Locomotor Movements closely resemble streaking and terrestrial bouncing which are seen during flight from human beings and other sources of harassment (Wilson, unpublished). Repeated leaping (porpoising) is often seen during rapid transit. It occurs in mothers of *P. v. vitulina*, when they desert and later return to their pups (Wilson, 1974b). It is used by sea lions, *Zalophus californianus*, in flight from aquatic predators (Norris and Prescott, 1961), and probably also by *Phoca*.

The caviomorph play jump resembles the stiff-legged bounding (stotting) of ungulates and the mara, *Dolichotis patagonum* (Smythe, 1971) which occurs when the predator has given up the chase or is not too close (Schaller, 1967). Smythe (1971) suggested that the function of stotting is to attract the predator's attention when the animal is far enough away to flee successfully. Stotting is also thought to alert conspecifics to the presence of a predator. Certainly stotting is a conspicuous display and probably has more signal value than does running. By the same token, play jumping may have more signal value than play running.

The rarity of Locomotor Movements in the play of *Ailuropoda* (except for running) and their frequency in the rodents and *Phoca* correlates directly with the presumed level of predation on the different species. The giant panda does not seem to have any major predators in the high-altitude bamboo forests, while the rodents and seal are preyed upon by larger carnivores.

Rotational Movements of the head or trunk also resemble behaviors seen in other functional contexts. The lateral head-shake is similar to the head-shake seen after an

animal sniffs a noxious olfactory stimulus; Andrew (1964) considered this a "protection response."

Although the head is rotated laterally in *Octodon* and *Octodontomys*, a vertical component was occasionally present in *Pediolagus* (head toss). Many ungulates display a head toss at the start of an escape leap or run (Eisenberg, personal communication). The head toss and head shake have also been distinguished in the play of juvenile black-tailed deer (Müller-Schwarze and Müller-Schwarze, 1969).

Eliciting stimuli

Olfactory stimuli. In the caviomorph rodents, Locomotor-Rotational Movements followed the perception of conspecific odor more frequently than any other stimulus. Such specificity of response was not found in *Phoca*, *Choeropsis*, and *Ailuropoda*, although body odor investigation was enhanced during play.

Rotational Movements, e.g., head shakes, were more common following olfactory stimulation than were Locomotor Movements, especially running. Perception of strong odors in non-play contexts also may result in head shakes, as already mentioned (Andrew, 1964). In *Ailuropoda*, head shakes, occasionally accompany scent-marking behavior. Young caviomorph rodents sometimes perform a slow head shake when auto-grooming.

Anti-predator responses may be elicited solely by predator odor. The chital, sambar, *Cervus unicolor*, and blackbuck, *Antelope cervicapra* (Schaller, 1967; Eisenberg and Lockhart, 1972) will bark, hoof stamp, stott, and then run when entering an area through which a predator has passed recently.

Although Locomotor-Rotational Movements during play were most often elicited by specific olfactory stimuli from group members, they may also occur in response to a "sudden stimulus contrast" (as suggested by Eisenberg and McKay, 1974, for anti-predator behavior). The rabbit, *Oryctolagus cuniculus* (Southern, 1948), agoutis, *Dasyprocta punctata*, maras (Smythe, 1970), and the chital (Schaller, 1967) have been ob-

served to perform Locomotor-Rotational Movements just before or after the onset of a heavy rain. Probably there is a sudden increase in the intensity of certain environmental odors under these conditions.

Visual stimuli. It has been suggested that Locomotor-Rotational Movements are contagious (Frädrieh, 1965; Ewer, 1966; Schaller, 1957, for the chital, *Axis axis*; Tyler, 1972, for wild ponies; Harper, 1973, for guinea pigs, *Cavia porcellus*). This implies that an animal performs such movements after seeing a conspecific do so.

In the caviomorph rodents, such movements were rarely followed directly by the same behavior in a nearby animal (see Section II-F-4), although this did occur in *Phoca*. The apparent visual contagion may result from two or more animals being active simultaneously, although in fact responding to other stimuli. For example, Harper (1973) concluded that head shakes were contagious in juvenile guinea pigs. However, he did not investigate behavioral sequences but compared numerous acts occurring in successive 10-sec intervals.

Contagion of a more general nature may be effective over the period of an activity bout. For example, *Octodon* and *Octodontomys* juveniles sometimes "joined in" with a playing dyad. Whether or not the effect is entirely visual is unclear. Schaller (1967) suggested that, during stotting in ungulates, odor may be released from the interdigital glands and this influences the behavior of nearby conspecifics. Interdigital glands do exist in mice (Ropartz, 1966) and probably also in the vole (Wilson, 1973), although their occurrence in *Octodon*, *Octodontomys*, and *Pediolagus* has not been investigated.

The rolling of the giant pandas seems to have a general contagious effect, but here the distinction between contagion and the response to play soliciting becomes blurred.

Tactile and auditory stimuli. Only *Phoca* employed a tactile stimulus, the Head-Over-Back posture, in the invitation and maintenance of play. The rodent naso-body contacts may constitute a tactile stimulus to the sniffed animal, who may or may not respond by participating in a play bout. Play interactions involved tactile contact in all the

species (including *Ailuropoda* when contact was permitted).

Auditory stimuli were absent during play of the larger species, *Octodontomys* and *Pediolagus*. A soft, purring vocalization ("gurgling," see Fig. 8b and Appendix 1, II) always occurred during mutual dyadic play interactions of *Octodon* (see below).

Play soliciting and "metacommunication"

A behavior pattern which is specific to the play context, unambiguous in meaning and elicits a play response in a conspecific is usually referred to as a "play soliciting" signal. Such signals are said to serve a "metacommunicative" function, in that they inform conspecifics of the "playful" intention of the sender, no matter what the normal function of the behavior patterns which are to follow (Bateson, 1956; Altmann, 1962; Bekoff, 1972).

In the six species we observed, there were both visual stimuli (Locomotor-Rotational Movements in *Octodontomys* and *Pediolagus*, Rolling in *Ailuropoda*) and tactile stimuli (the Head-Over-Back signal of *Phoca*) which appeared to elicit play from conspecifics. In *Octodon*, whose play lacks the frequent Locomotor-Rotational Movements found in *Octodontomys*, prolonged dyadic interactions were always accompanied by "gurgling" (see Fig. Bb), a soft continuous vocalization, which may also have a metacommunicative function, substituting in this respect for Locomotor-Rotational Movements.

Although sniffing conspecific body odor typically results in Locomotor-Rotational Movements in the rodents, such a stimulus has not been considered comparable to a play-soliciting signal since body odor is not thought to contain a message exclusive to play and body odor is unlikely to be released voluntarily to solicit play. However, this possibility should not be entirely excluded since we understand little about the variety of odors which can be produced by a single individual or the signal values of these odors.

There is a paradoxical effect of the performance of Locomotor-Rotational Move-

ments during play, in that they signal both the playful intent of the performer and result in temporary termination of play bouts and, hence, an immediate decrease in sensory input to the performer from conspecifics. Jumping, head-shaking, and running all involve a "cut-off" of stimulation to the performer and resemble the "cut-off" postures described for other contexts by Chance (1962) and discussed by Barnett and Evans (1965). Possibly this serves to terminate ongoing activity before sensory input reaches "noxious" levels. Since Companion-Oriented play bouts tend to be terminated by this behavior, the Locomotor-Rotational Movements by one animal affects both partners. However, since play bouts tend to be one-sided (see item 5 under *Sequencing Behavior* above), the impact of the "cut-off" effect is greatest on the performer. In Solo Play, of course, only the performer is involved. For example, in *Octodontomys*, Mutual Upright interactions prolonged by one partner often lead to high-pitched squeaking and escape by the other. Of course, during the heightened activity resulting from Locomotor-Rotational Movements, the animals are rapidly reunited and stimulus input is renewed. In other contexts, such as sniffing noxious or predator's odors, similar movements result in a more long-lasting termination of input.

One question which still remains is why the young are so much more responsive to body odors and other stimuli than are adults. It may be that olfactory thresholds of the young are lower than those of adults, thus conspecific odor may be a relatively stronger stimulus or provide more stimulus contrast to the young. This may account for the common statement that young animals are "hyperexcitable" and would contrast with the hypothesis that play is caused by a "need" to perform particular kinds of acts (see Ewer, 1968, for a discussion). More emphasis in future studies should be directed to play serving as a means of enhancing and controlling sensory input by the investigation of the environment and conspecifics and by the proprioceptive feedback occurring during the performance of play movements.

The role of play in the development of social behavior

Whether body odor sniffing elicits Locomotor-Rotational Movements or whether it occurs during the heightened Companion-Oriented activity which follows play soliciting, the effect is the same; sniffing the body odors of the parent, offspring, or group members is enhanced during play.

One result is both immediate and more protracted learning of the identity of the partner. Immediate learning of identity seems to be one of the functions of the play between the seal mother and her pup. Play, including naso-body contact develops during the first week post-partum and probably contributes to the development of mutual recognition, essential to the pup's immediate survival.

In adolescent seals, naso-body contact occurred less frequently than in mothers and pups, suggesting that mutual recognition is less immediately critical. However, long-term learning of the olfactory characteristics of conspecifics may be important in the development and maintenance of the subgroups which seem to exist within the herd (Wilson, unpublished).

In family groups of *Octodontomys*, both parents and young, after awakening, immediately engage in intense social activity and do not eat until much later. This suggests that, in the natural state, family groups (probably without the father) may play together close to the nest site and then disperse to forage. The coupling of olfactory-related activities, such as sandbathing, urinating, and naso-body contact with play might serve to strengthen group cohesion on a nightly basis as well as aiding in the formation of long-term social attachments between naive young. The importance of sibling odor in the development of social attachments of young laboratory rats is paramount (Marr and Williston, 1969).

The level of participation by the father in play in *Octodon* and *Octodontomys* provides an interesting contrast which also supports the suggestion that play in these rodents is involved in learning the odor characteristics of conspecifics. *Octodon* lives in

extended family groups and in captivity the male exhibits extensive parental care by grooming and huddling over his offspring. Thus, a sharing and learning of individual odors would occur in the nest. The *Octodon* male rarely plays with his offspring. By contrast, the *Octodontomys* father only occasionally squats over the young or grooms them, but does play with them (Wilson, unpublished). Since *Octodontomys* males probably do not cohabit permanently with a single female, adult males may only encounter young on an irregular basis. Play with the young would permit a rapid exchange and learning of odors.

One further, less tangible, possibility concerning the function of the kind of play we have observed is that early learning about the characteristics of group members is enhanced in such a way that social behavior at a later stage in development may be more adaptable, as has been suggested by Barnett and Evans (1965). As an example, the sexual preferences of female laboratory mice are strongly influenced by early learning of the parents' odors (Mainardi et al., 1965). This is also true of laboratory rats (Marr and Gardner, 1965).

Another example has been suggested for the vole where young born early in the breeding season (spring) nosed one another and played more than young born towards the end of the season (autumn) (Wilson, 1973). The spring-born young comprise the autumn breeding cohort and juvenile survival is high in the autumn while the offspring of autumn-born voles born the following spring show poor survival (Chitty and Phipps, 1966). This variation in juvenile survival may result from differing levels of aggression in adults and especially in adult males, with spring-born animals exhibiting more tolerance of young and other conspecifics due to their more frequent play activity as juveniles.

APPENDIX I. PLAY AND ASSOCIATED PATTERNS OF *Octodon degus*, *Octodontomys gliroides*, AND *Pediolagus salinicola*

I. Locomotor-Rotational Movements.

A. Head-shake (*Octodon*, *Octodontomys*, *Pediolagus*).

Vigorous lateral movement of the head, sometimes

with a vertical component (most noticeable in *Pediolagus*) which gives the appearance of a toss, jerk, or nod. Headshakes vary in tempo and duration.

B. Body twist (*Octodon*, *Octodontomys*, *Pediolagus*).

One part of the body (between the neck and tail) is twisted with respect to another part, at high intensity, appearing to be a serpentine wave travelling the length of the body. Forequarters twisting is often coupled with a head shake and appears to be an extension of the head shake. The degree of lateral movement in the twist may denote intensity.

C. Jump (*Octodon*, *Octodontomys*, *Pediolagus*) (Fig. 4).

A leap or spring in which all the limbs leave the ground. A considerable height is achieved and usually a relatively small distance is covered. In *Pediolagus* occasionally a "rear-up" was observed, when only the forelegs left the ground. Since this was relatively uncommon, it was lumped with jumping.

D. Turn (*Octodontomys*, *Pediolagus*) (Fig. 5).

Usually occurring during a jump and resulting in the animal's facing a different direction upon landing. The angle of the turn varies up to about 180 degrees.

E. Run (*Octodon*, *Octodontomys*, *Pediolagus*).

Differs from the running of "normal" locomotion by the addition of an exaggerated vertical component. Also a play run may describe an arc (particularly in *Octodon* and *Octodontomys*) rather than a straight line, and may lack orientation to a goal. *Pediolagus* often run with high, mincing steps.

F. Hind-leg kick-back (*Pediolagus*, seen once in *Octodontomys*).

Kicking the hind-legs backwards and upwards during a jump or run. The perineal area is conspicuously displayed.

II. Integrated Companion-Oriented Patterns in *Octodon degus*, *Octodontomys gliroides*, and *Pediolagus salinicola*, which frequently lead to Locomotor-Rotational Movements.

(The approximate age the behavior was first seen is indicated in parentheses.)

A. Naso-Body Contact Forms.

1. Single naso-body contact, *Octodon* (day 3-8), *Octodontomys* (day 2-5), *Pediolagus* (day 1).

An animal approaches another, noses its body, immediately gives Locomotor-Rotational Movement and withdraws.

(a) Riding. *Octodontomys* young were clearly excited by nosing the parents' (particularly the mother's) napes. They would climb on to the parent's back and thrust the nose vigorously into the fur of the nape and the side of the neck, giving head-shakes and often body twists before withdrawing. The parents were usually passive. Sometimes the young kneaded the parent's back with its feet. Pelvic thrusting was added to this behavior around 2 months of age (by the male young).

Similarly, in *Octodon* young, one juvenile would approach the other, nose its nape while placing its forepaws on the other's back, and then climb

on its back (first seen in the second week). The animal underneath then usually began to move with the other riding on it, its nose still buried in the fur of the other's nape (Fig. 8Bh). Occasionally the riding animal was simultaneously ridden by a third animal. Locomotor-Rotational Movements accompanied this behavior only occasionally, but a "gurgling" vocalization was common (see VI-B-3 and 4). The ridden animal was usually the one to withdraw, sometimes sandbathing underneath its rider. Pelvic thrusting was seen in males from about 6 weeks and very occasionally occurred in infancy. This behavior was also seen outside a play context (e.g., between two unfamiliar young in a strange enclosure; between father and young, with the father pelvic thrusting; within stable groups of adolescents).

2. Multiple naso-body contact: *Octodon* (first or second week), *Octodontomys* (second or third week), rare in *Pediolagus*.

An approach followed by a series of naso-body contacts in rapid succession. Different parts of the body may be nosed in no predictable sequence. The approached animal may reciprocate but nosing is usually predominantly shown by one animal. Locomotor-Rotational Movements are often given by *Octodontomys*, but less often by *Octodon*, during one or between two nosing contacts. These movements are usually given by the nosing animal, less so by the nosed animal. "Gurgling" sometimes occurs in *Octodon*. A third animal may join in, especially when an *Octodontomys* young joins its sibling and a parent playing together.

(a) The Mutual Upright: *Octodon* (second week), *Octodontomys* (second-third week).

The dyad simultaneously adopts the bipedal position, with the naso/mouth area of each animal in contact and both pawing with the forepaws. One or both of the pair may exhibit Locomotor-Rotational Movements; this is much more frequent in *Octodontomys* than in *Octodon*. Gurgling always accompanies this behavior in *Octodon*.

The degree of body tension and lateral body swaying varies. The body of one or both of the dyad may become tense, with the forepaws of the animal pushing against the other's shoulders. The bodies strain against each other forming an inverted V (mainly in *Octodon*) and a dyad may sway from side to side (more characteristic of *Octodontomys*). If separation does not occur, one of the pair may emit high pitched "protest" squeaks until they do. At this point "gurgling" ceases to occur in an *Octodon* dyad. In *Octodontomys*, the squeaking young would sometimes run to the mother and crouch or lie supine beside her.

Occasionally one animal (*Octodontomys* only) appeared to solicit the Mutual Upright interaction by approaching, making naso-mouth contact, and attempting to push the other animal into the upright position (commonest between a juvenile and a parent). Usually, however, the position seemed to be adopted spontaneously and simultaneously by both animals. It could occur either at the start of a play bout or interrupt a Multiple Nosing Contact play bout.

(b) Mutual Upright with Incisor Interlocking:

Octodontomys (fourth-sixth week).

The dyad adopts the bipedal position, makes mutual naso-mouth contact and immediately interlock their incisors at right angles. This incisor-lock may be held for several seconds, during which time the animals may run and climb around together. Locomotor-Rotational Movements did not accompany this behavior; probably they would be a physical impossibility.

(c) Supine-Quadrupedal: *Octodontomys* (second-third week), rarely in *Octodon* (but seen on day 6 in Litter IX).

One animal lies on its back while the partner, standing quadrupedally to one side, maintains continuous naso-mouth contact. Either or both may give Locomotor-Rotational Movements.

The Supine-Quadrupedal interaction may arise out of a Multiple Nosing Contact sequence or develop from the Mutual Upright interaction. Occasionally it was apparently solicited by one animal approaching another and lying supine beside it, the other then making naso-mouth contact with it and adopting the upright role. Role reversal was not seen during these interactions.

(d) Circling: *Octodon* (fourth-seventh week).

Reciprocal nosing of the nape region by a dyad while moving round one another (occasionally seen between unacquainted juveniles in a strange enclosure), usually accompanied by "gurgling." Sometimes the two animals seemed to be pushing each other as they circled. Although this behavior is usually dyadic, three young of Litter II (day 27) were observed moving in a circle, each nosing the nape of the animal in front. Circling with reciprocal nosing of the rump region was also seen occasionally.

III. Non Companion-Oriented patterns which may lead to Locomotor-Rotational Movements.

A. Sandbathing: *Pediolagus* (day 1), *Octodontomys* (second-third week), *Octodon* (second-fifth week).

The animal rubs the flank in the sand, either once, or several times, alternating the side of the body in *Octodon* and *Octodontomys*. In *Pediolagus* this is often preceded by dragging the venter forward in the sand. Sites on which urine and anal gland secretion have been deposited are preferred (Kleiman, 1974; Wilson, unpublished). In *Octodon*, sandbathing rarely occurs in the context of play except during Riding (by the animal being ridden). In *Octodontomys*, sandbathing may occur in or out of a play context as judged by other criteria. In *Pediolagus*, sandbathing may result in either the actor or another animal giving Locomotor-Rotational Movements. *Octodontomys* young sometimes engage simultaneously in a bout of vigorous sandbathing in contact with one another, e.g.:

1 male and 1 female young of Litter II (d. 69): male pulls female's tail; female sandbathes twice; male approaches her; female sandbathes twice; male sandbathes three times beside her; female sandbathes once; male sandbathes once; female sandbathes once; male sandbathes once; female sandbathes once and runs away; male sandbathes three times; approaches female; pulls her tail; noses her nape; male sandbathes once.

The family members may often sandbathe in the same locus one after the other, especially just after awakening. This was not necessarily associated with play.

B. Urinating and sniffing urine (*Pediolagus, Octodontomys*, does not occur in a play context in *Octodon*).

Pediolagus urinates by squatting and (a) squirting urine in quantity onto the substrate, or (b) touching the perineum to the substrate, moving the hind-quarters from side to side or dragging forwards, and then excreting a small quantity of urine. Anal gland secretion may be released during perineal dragging and rubbing. Urine squirting, perineal dragging, and digging at urine-saturated sand with the fore-paws frequently results in Locomotor-Rotational Movements, either by the actor or by a nearby animal.

Octodontomys urinating posture is not always obvious. Usually the rump is raised slightly, often near a corner, and urine is squirted in large quantity onto the substrate. This is sometimes followed by dragging the perineum along the ground. Urinating and perineal dragging are very occasionally associated with play by the actor, e.g.:

Solo play by a female young of Litter III (day 31): Sandbathes, rolling right over; jumps; perineal drags; sandbathes once; perineal drags; jumps; digs in sand.

APPENDIX 2. PLAY INTENSITY SCORES FOR LITTERS OF *Octodontomys gliroides*

The different behavior patterns during play were given numerical values, based on their presumed "intensity," and summed to produce a symbolic score. This score comprised Locomotor-Rotational Movements and the nosing contacts preceding it,

as well as Mutual Upright and Supine-Quadrupedal interactions, Riding, Circling, and Tail Pulling. The basic scoring method is given below.

Activity	Score
Single Locomotor-Rotational Movement not preceded by nosing contact	1
Multiple or Intense (with body twist) Locomotor-Rotational Movement not preceded by nosing contact	3
Single Locomotor-Rotational Movement preceded by nosing contact	2
Multiple or Intense Locomotor-Rotational Movement preceded by nosing contact (For prolonged nosing, add 1 to the above scores.)	4
Mutual Upright or Supine-Quadrupedal without Locomotor-Rotational Movement	4
Mutual Upright or Supine-Quadrupedal with Locomotor-Rotational Movement (both animals)	6
Mutual Upright or Supine-Quadrupedal with Intense Locomotor-Rotational Movement (both animals)	10
Mutual Upright with Incisor Interlocking without Locomotor-Rotational Movement	3
Tail nibbling/pulling	2
Tail pulling from side to side, up, down or round obstacle	3
Pulling companion along by tail	4
Continuous tail pulling	6
(per ca. 30 sec)	
When Locomotor-Rotational Movement accompanies tail play, add appropriate score.	

APPENDIX 3A. TWO-ACT SEQUENCES DURING PLAY BY THE YOUNG OF *Octodontomys* LITTER V (2 ♀♀)

Act following	Act preceding														Indiv.	
	Ap	B	R	N	Uprt	Sup	T	T pull	J	Run	Mov	Roll	Sep	Total	Total	
Ap ₁								6	3	1	1		34	11	57	
Ap ₂									3	1	1	7		12		
B ₁	74	16	3			0	2	0	18	1	22	3	0	139	185	
B ₂	8	5	0			2	0	1	1	0	1	2	0	20		
R ₁	11	4	1			0	2	2	2	0	4	0	0	26	31	
R ₂	0	1	0			0	0	0	0	0	0	0	0	1		
N	33	3	1	2	0	1	2	3	2	1	4	1	0	53	53	
Uprt	2	9	0	0	0	1	1	0	0	0	1	0	0	14	14	
Sup ₁	0	0	0			0	0	0	0	0	0	0	0	0		
Sup ₂	1	3		0	0								0	4	8	
T ₁	12	5	2			0	1	0	1	0	4	0	0	25	27	
T ₂	1	0	0			0	0	0	0	0	0	0	0	1		
T pull ₁	17	0	0			0	0	2	2	2	1	0	0	24	29	
T pull ₂	2	1	0			0	0	0	0	0	1	0	0	4		
J ₁	8	40	4				9	3	1	2	4	0	0	71	112	
J ₂	2	4	0				0	2	1	1	4	2	0	20		
Run ₁	1	5	0			0	0	0	3	0	3	1	1	13	21	
Run ₂	0	1	0			0	0	0	1	0	1	3	0	6		
Mov ₁	4	88	8			2	10	3	2	2	1	0	2	120	158	
				15	5								2			

Mov ₂	1	7	0			2	0	2	2	0	2	0		16
Roll ₁	2	4	0			0	0	0	5	1	2	0		14
				0	1								4	28
Roll ₂	0	1	0			1	0	0	2	1	1	3		9
Sep	9	89	18	17	6	4	11	13	44	3	90	3		284
Indiv.														307
Total	189	285	37	2	0	13	38	32	99	18	148	26		887
Total	190	288	37	73	19	14	38	32	100	18	148	26	47	1030

APPENDIX 3B. TWO-ACT SEQUENCES DURING PLAY BY THE YOUNG OF *Octodontomys* LITTER II (1 ♂, 1 ♀)

Act following	Act preceding													Indiv.	
	Ap	B	R	N	Uprt	Sup	T	T pull	J	Run	Mov	Sep	Roll	Total	Total
Ap ₁									5	0	1	25		31	44
Ap ₂												3			
B ₁	49	15	3						2	0		8		10	
B ₂	1			21	7				8	3	5	0	6	99	152
R ₁	9	2	2			1	0	0	3	0	3	1	1	22	
R ₂	16	5	2			0	0	3	1	1	2		2	32	42
N				5	1								1	4	
Uprt	0	0	0			0	0	1	0	0	1	1	1	4	
Sup ₁	53	14	5	10	1	0	0	2	3	0	5		0	93	93
Sup ₂	19	9	1	2	1	1	0	0	5	0	3		2	43	43
T ₁	1	0	0						1	0	2		0	4	13
T ₂				1	3										
T pull ₁	1	3	1			0	0	0	0	0	0		0	5	
T pull ₂	4	0	0	0	0	0	0	1	1	0	3	1	4	14	17
J ₁	1	1	0	0	0	0	1	0	0	0	0	0	0	3	
J ₂	21	9	3			0	0	2	7	2	0	1	4	49	66
Run ₁				4											
Run ₂	5	2	3			0	0	1	1	0	0	0	0	12	
Mov ₁	9	22	2			0	2	1		1	1	4	0	42	
Mov ₂				26	5							1	1	93	
Sep ₁	6	2	1			0	1	2	1	0	0	4	1	18	
Sep ₂	2	2	0	0	0	0	0	1	0	1	0	0	0	6	11
Roll ₁	1	0	0	0	0	0	1	0	0	0	1	2	0	5	
Roll ₂	1	0	0											41	93
Indiv.				1	17				1	2	1	0	0	11	
Total	2	4	1			2	4	23	18	1	0	0	0	101	
Total	4	25	5			2	4	23	18		22			265	
Total	3	8	3	21	25			7	11		1			86	
Total	3	23	4			2	4	14	12		24		1	8	31
Total	1								1	1	1	19	0	23	
Total	211	165	38	12	2	8	20	63	67	7	76	67	26	762	
Total	212	174	42	113	60	10	20	70	78	7	78	72	27	963	

APPENDIX 3C. TWO-ACT SEQUENCES DURING PLAY BY THE YOUNG OF *Octodon* LITTER VII (4 ♂♂; 2 ♀♀)

Act following	Act preceding											Total
	Ap	B	R	N	Uprt	Rid	Circ	J	Mov	Sep	Total	
Ap											19	19
B	34	52	8	37	53	8	4	8	28			232
R	4	6	0	2	2	0	0	0	1			15
N	32	34	2	19	8	4	0	7	13			119
Uprt	17	37	0	16	61	3	1	2	26			163
Rid	7	10	0	6	6	12	1	1	3			46
Circ	1	0	0	1	1	5	0	0	0			8
J	0	13	1	9	4	1	1	10	6			45
Mov	0	55	1	20	12	2	0	3	16			109
Sep		27	3	4	18	12	1	15	11			91
Total	95	234	15	114	165	47	8	46	104	19		847

APPENDIX 4. BEHAVIOR PATTERNS DURING SOCIAL PLAY OF ADOLESCENTS AND OF MOTHERS AND YOUNG OF *Phoca vitulina concolor* (Behavior patterns described in the text are listed here)

A. Head-Over-Back Contact (play soliciting signal).

B. Naso-body Contact. This occurs on the beach and in the water.

C. Mutual Stroking. The dyad stroke, scratch, and pat one another with the foreflipper. This occurs only on the beach.

D. Lunging. One animal may lunge, with closed or open mouth, at the other's head, nape, or throat. This behavior is relatively rare, and occurs only on the beach.

E. Rolling. Two animals somersault over one another in almost continuous contact (see Wilson, 1974a, for detailed description of this behavior). This occurs only in the water.

F. Locomotor-Rotational Movements. Rotational Movements (adolescents, $n = 20$; mother and pups, $n = 4$) included lateral movements of the whole trunk or only of the hindquarters (described as "wiggling" when the amplitude was small and "thrashing" when the amplitude was considerable); lateral head shaking, occasional vertical head tossing; and waving of the head and foreflippers. One adolescent was seen to leap out of the water and roll on its own axis while airborne.

Locomotor Movements (adolescents, $n = 75$; mother and pup, $n = 80$) were more common than Rotational Movements, and included rearing out of the water, either forward, sideways or backwards; "torpedoing" along just under the surface, sometimes with a sudden change in direction; "whooshing" along the surface, often with the incoming surf; and "hovercrafting" along just above the surface with considerable splashing. Bouncing and flopping along occurred occasionally on the beach.

(The n 's include only the Locomotor-Rotational Movements of the longer play bouts used in this analysis.)

Because of the great variability in form and their relative infrequency during Companion-Oriented play (see Fig. 7), Locomotor-Rotational Movements were not subdivided in the analysis.

G. Porpoising and Splashing. It was common for adolescents of a separated dyad, or who had not formed a dyad, to display a prolonged series of por-

poising off-shore with splashing of both the fore and hind flippers, the splash usually producing a loud report as well as a shower of spray.

APPENDIX 5. BEHAVIOR OF MOTHER AND CALF, *Choeropsis liberiensis*

I. Behaviors not specific to play.

a. Body-to-Body Contact.

Both mother and calf initiated this contact, which did not involve the muzzle. Commonest were head-to-head, head-over-back, and head-under-chin contacts.

b. Pushing.

The mother propelled the calf in front of her, either with her nose to part of its body or with her chin over it. Sometimes she pushed it into the water from the step or pushed it away from the step.

c. Naso-Body Contact.

Most frequent were nose-to-side of neck, head, and cheek. The flank and rump were also nosed. There is a pore in the posterior region of the lower jaw in the female, which does not open until puberty (Eisenberg, personal communication). Doubtless secretion from this pore is involved in nosing contacts and chin and cheek rubbing (see [d] below).

d. Chin and Cheek Rubbing (first seen by both young and mother on day 33).

Both mother and calf rubbed the steps with the chin or cheek.

e. Defecating.

The mother defecated by agitating her tail while she excreted loose feces, thereby producing a wide-ranging shower of fecal matter. She usually defecated against the wall, over the calf, or both. The calf did not defecate in this manner during the observation period.

f. Sniffing and Chewing (first seen on day 27).

The calf frequently nuzzled and chewed mother's feces. She also nuzzled the step where the mother had chin or cheek rubbed. The mother occasionally sniffed her own feces.

II. Play Behaviors.

g. Muzzle-to-Muzzle Contact.

h. Locomotor-Rotational Movements.

A variety of body movements accompanied the calf's behavior. These were: head shake, head toss, stretching head up, body undulating, pirouetting on hind legs, submerging with corkscrew action of head, and leaping out of the water. Lateral head shake or swing and head stretching occasionally oc-

Legend to Appendix 3:

AP = approach; B = nape nosing contact; R = rump nosing contact; N = naso-nose/mouth contact; Uprt = Mutual Upright interaction; Sup = Supine Quadrupedal interaction; Rid = riding; Circ = circling; T = tail nosing contact; T pull = tail pulling or nibbling; J = jump; Run = running; Mov = Rotational Movement; Roll = sandbathe; Sep = separate.

Subscript ₁ = first animal; subscript ₂ = 2nd animal; figures between 1 and 2 indicate that the active or initiating individual was not distinguished; Individ total = totals where individuals could be distinguished; Total = totals including double activities (such as N and Upright) and activities where the individuals were not distinguished.

The underlined cells indicate significant linkages. The linkage was taken to be significant if the difference between the observed and expected values was greater than three times the square root of the expected value (McKinney, 1961).

curred on the part of the mother.

Locomotor-Rotational Movements were not subdivided into categories of body and locomotor movements in this analysis because of the small number of observations of Locomotor-Rotational Movements (see Appendix 5b).

i. Water Agitating (Splashing).

The mother agitated the water by swinging her head or head and body vigorously through the water. Most often the head swinging created a great deal of splashing. Occasionally more gentle head swinging, or moving the head up and down, created small waves, and appeared to encourage the calf to follow the mother. The calf occasionally made small splashes with its head, body, or forefoot.

j. Lying with Head or Head and Body on Side (first seen day 38).

The mother lay on her side when she approached the calf and initiated contact with it. Her mouth was open just sufficiently to expose the teeth, and sometimes wider. Her body tone was markedly relaxed. Very occasionally the calf approached the mother on its side.

k. Gaping (first seen by the mother on day 33, and by the calf on day 31).

The mother gradually opened her mouth and stretched her head up, raising her lower jaw out of the water. The degree of gape finally reached varied, the maximum resulting in the mouth being opened to its fullest extent and the head and shoulders being raised right out of the water. Gaping was usually oriented towards the calf. The calf gaped much less often than the mother. Her gaping was not subtly graded like the mother's, but consisted simply of opening and shutting the mouth.

Verheyen (1954) has given a detailed description of this behavior in non-play contexts in the Nile hippopotamus (*Hippopotamus amphibious*) in which the complete gaping was exclusive to adult males.

l. Jaw Nibbling (first seen by the calf on day 39).

The calf nibbled the upper and lower jaws of the mother when she was gaping, often stretching up or jumping up to reach her mouth. Nibbling at the muzzle region could also occur by either mother or calf when the nibbled animal was not gaping.

APPENDIX 6. TWO-ACT SEQUENCES DURING PLAY OF THE PYGMY HIPPOPOTAMUS, *Choeropsis liberiensis*

Act following	Act preceding													Total
	a	b	c	d	e	f	g	h	i	j	k	l		
a	<i>34</i>	6	16	2	10	6	4	18	8	13	3	1	121	
b	4	4	7	1	5	1	1	4	0	1	1	0	29	
c	14	2	<i>37</i>	2	3	3	9	15	4	16	7	3	115	
d	2	2	2	4	0	0	0	5	1	5	1	0	22	
e	9	1	7	2	0	3	4	8	3	2	1	2	42	
f	0	1	4	0	<i>12</i>	5	3	6	1	0	6	1	39	
g	5	0	4	0	6	4	3	9	1	5	5	0	42	
h	24	1	22	1	5	9	3	30	5	9	14	3	126	
i	2	2	5	2	2	1	0	7	9	0	1	0	31	
j	6	2	9	2	2	2	5	11	1	5	2	1	48	
k	8	0	11	3	0	0	12	14	0	3	9	7	67	
l	1	0	0	0	0	0	2	0	0	1	15	2	21	
Total	109	21	124	19	45	34	46	127	33	60	65	20	703	

The italic cells indicate significant linkages. The linkage was taken to be significant if the difference between the observed and expected value was greater than three times the square root of the expected value (McKinney, 1961). a-l are behavior components as given in Appendix 5.

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