

COMPARATIVE ONTOGENY OF SOCIAL BEHAVIOUR IN THREE SOUTH AMERICAN CANIDS, THE MANED WOLF, CRAB-EATING FOX AND BUSH DOG: IMPLICATIONS FOR SOCIALITY

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Abstract. Aspects of behavioural development were investigated to determine how a relatively social canid like the bush dog *Speothos venaticus* differs from the moderately social crab-eating fox *Cerdocyon thous* or the relatively solitary maned wolf *Chrysocyon brachyurus*. Differences emerged that were surprising in light of conventional ideas about sociality. The behavioural repertoire of *Speothos* was more limited than those of the other two species and *Speothos*' interaction sequences were simpler, comprised fewer different elements, and were more rigidly determinate. Submissive behaviours, biting, vocalizing, and object play were prominent in *Speothos*. *Cerdocyon* and *Chrysocyon* interaction sequences were more like the play behaviour described for *Canis* species, being characterized by vigorous wrestling, frequent switching between behavioural categories, and manoeuvring to upset the partner. Although *Speothos* pups spent a greater percentage of their time interacting, there were no interspecific differences in the length of interaction sequences. In contrast to what has been seen in some polygamous mammals, no sex differences in behaviour were found here, indicating that in monogamous, monomorphic species with little adult social role differentiation, the young are behaviourally alike as well. Dominance hierarchies among pups were only very weakly indicated and unstable in these intact litters raised by both parents.

The comparative ontogeny of social behaviour in taxonomically related animals having divergent social organizations is of interest in revealing possible developmental pathways to sociality. In polygynous, dimorphic species with extensive divergence in adult male and female roles, early sex-related differences in juvenile play and aggressiveness have been identified (primates: Hinde & Spencer-Booth 1967; Kummer 1968; Symons 1978; ungulates: Berger 1979, 1980). In the North American canids, which are largely monomorphic and show relatively little divergence in male and female behaviour (Kleiman 1977), juvenile sex differences are minimal (Bekoff 1974). Bekoff has related species-typical differences in the early aggressiveness of canids to later dominance and hierarchy formation and the degree of sociality in the species. The present study of South American canids examines many parameters of early social behaviour in an attempt to identify those that are most characteristic, or predictive, of later social differences. Potential sources of interspecific variation investigated here include frequency and length of interactions, tendency to interact in groups, and

differences in the types of behaviours seen, their frequency, sequencing, or differential expression by males and females.

The maned wolf (*Chrysocyon brachyurus*), crab-eating fox (*Cerdocyon thous*) and bush dog (*Speothos venaticus*), while all monogamous, display a divergence in social organization that is representative of all major categories of sociality in the family Canidae. The field data on *Chrysocyon* indicate that this is a solitary species, with male and female in close association only during the breeding season (Kreig 1940; Dennler de la Tour 1968; Dietz 1981). The mated pair remain together for some time after the birth of pups (Dietz 1981). *Chrysocyon* individuals maintain home ranges of up to 30 km² in their native Brazilian Highlands (Dietz 1981) and like-sexed adults are generally intolerant of each other in captivity (Brady & Ditton 1979). These largest of the South American canids are omnivorous, but take prey no larger than can be handled by a single individual, e.g. *Agouti paca* (Dietz 1981). Cooperation in hunting has not been observed. Although some canids previously considered typically solitary have recently been shown to associate in family groups (red fox, *Vulpes vulpes*: Macdonald 1979) or even packs (coyotes, *Canis latrans*: Camenzind 1978; Bekoff & Wells 1980), no such evidence exists for *Chrysocyon*. Thus

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Chrysocyon appears to be among the least social of the canids.

The mated pair is the modal social unit of *Cerdocyon* (Brady 1979), as is typical of most small or medium-sized canids that have been studied, e.g. the golden jackal, *C. aureus* (van Lawick 1971), black-backed jackal, *C. mesomelas* (Van der Merwe 1953), coyote, *C. latrans* (Camenzind 1978), and bat-eared fox, *Otocyon megalotis* (Lamprecht 1979). In most of these species, young remain with the parents for several months, and in some cases, e.g. *C. aureus* (van Lawick 1971) and *C. mesomelas* (Moehlman 1979), for over a year. *Cerdocyon* young disperse at about 5–8 months of age (Brady 1979). Mated *Cerdocyon* pairs forage in company, although not cooperatively; they share territorial defence and care of the young, and engage in mutual grooming (Kleiman & Brady 1978). They do not share prey, although males may provision their pregnant or lactating mates. No dimorphism is apparent and both sexes use a raised-leg stance (females forward, males back) when urinating. *Cerdocyon* is omnivorous, as are most of the other medium-sized canids mentioned (Kleiman & Brady 1978).

Observations of both free-living and captive *Speothos* indicate a social structure based on the extended family (Kleiman 1972) or pack (Bridges 1954). Walker (1975) mentions hunting by packs of bush dogs, and the specialized dentition of *Speothos* suggests a largely carnivorous diet (Kleiman 1972). Despite its small size (5–7 kg), *Speothos* attacks pacas (*Cuniculus*) and capybaras (*Hydrochoerus*) as large or larger than itself (Tate 1931; Langguth 1975; Ramos 1980), thus favouring cooperative hunting. In captivity, family groups cooperate to bring down large rabbits (Biben 1982b) and never fight over food. *Speothos* may be likened to other cooperatively-hunting canids (wolf, *Canis lupus*: Mech 1970; dhole, *Cuon alpinus*: Davidar 1975; Johnsingh 1980; African wild dog, *Lycaon pictus*: Estes & Goddard 1967) whose typical social units are the extended family group or pack. In all of these, a cohesive group is essential for bringing down large prey. Non-dispersing pups may form the basis of the group (Frame et al. 1979).

Methods

This study is based on data from two captive *Chrysocyon* litters (Ch1 and Ch2), two *Cerdocyon* litters (C1 and C2), and three *Speothos*

litters (S1, S2 and S3). All animals were housed at the National Zoological Park's Conservation and Research Center at Front Royal, Virginia. Both *Cerdocyon* litters were born to the same parents; *Chrysocyon* and *Speothos* litters were all born to different parents. Sex ratios were as follows (M:F): Ch1 (2:0), Ch2 (5:1), C1 (1:2), C2 (2:4), S1 (3:1), S2 (2:3), S3 (0:3). All pups were individually marked by fur clipping, collars, or dye. *Cerdocyon* and *Speothos* pups remained with both parents for the period of observation, which was 6 months for C1, C2, S1 and Ch1, 4 months for S2, 3½ months for Ch2, and 2½ months for S3. The S1 pups were hand-fed for several weeks when their mother failed to lactate sufficiently, but were not removed from the family group for more than a few minutes at a time. Because paternal behaviour is not documented for *Chrysocyon*, these males were separated from their mates shortly before parturition, and attempts were made to reintroduce them gradually after the birth. The Ch1 father showed solicitous reactions to the pups and was housed with them permanently from week 8. The Ch2 father was consistently aggressive to pups and was therefore kept separated from them.

Animals had access to indoor observation dens with nestboxes, and outdoor runs with natural vegetation. Litter S1, born in winter, used an indoor run for the first 4 months. All families received live prey at least once a week, in addition to their regular diet.

Data collection was by direct observation, often using a tape recorder, and averaged 150–200 min per week per litter. Animals were observed at times of day when they were most active. Time sampling of behavioural 'states' (Altmann 1974) at 10-s intervals, and data on sequences of behavioural acts (including the nature of the act, the sender, and the recipient) were recorded simultaneously for a focal animal. Time samples were used for determining the percentage of time spent in an activity; sequence data were used for analysis of frequencies of behaviours (number of occurrences). All data presented are for the entire period of observation, unless otherwise stated.

The terminology used here conforms, as much as possible, to common usage in the English language literature on canids. Behavioural repertoire descriptions are as in Bekoff (1972) except where noted, and abbreviations are given in parentheses for the following major categories:

Open-mouth gape (GA): the canid 'play face' and 'aggressive gape' are considered together here because of difficulty in distinguishing them out of context (Poole 1978).

Bite (BI): biting (all targets) and bite intention (no contact made) are considered together here.

Grapple (GR): wrestling on hindlegs or on the ground, animals on their sides.

Stand over (SO): the pup below may be prone or supine, upright or pressed to the ground, and quiet or struggling. The pup above is in any orientation. Juvenile 'mounting' or other sexual activity was rare, and virtually all instances of SO appeared to be non-sexual.

Roll over (RO): active and passive submission (Schenkel 1967) are considered together here.

Exaggerated approach or Exaggerated gait (EA): leaping about with a loose, bouncy gait. Included in this category is the 'play bow' (Bekoff 1977), which was common in *Chrysocyon*, rare in *Cerdocyon*, and absent in *Speothos*.

Chase (CH).

Paw (PW): pawing (all targets) and paw intention (no contact made) are considered together here.

Muzzle wrestle (MW).

Object play (OP): manipulation of objects by biting, carrying, tossing, and tug-of-war (Biben 1982a).

Lick, sniff (LI): includes muzzle sniffing, anogenital sniffing and grooming. *Speothos* rarely groomed self or others.

Vocalization (VO): mainly growls and whines.

Additional categories of limited occurrence include:

Fighting: in *Chrysocyon* and *Cerdocyon* this included hip slamming, biting, and attempts to unbalance or upset, accompanied by growls, squeals, and screams, while *Speothos* pups fought in the manner of adults, described by Kleiman (1972), except that pups growl during fights, while adults are silent.

Defence play: growling or gaping while in, or at entrance to, a protected cavity having no special significance at other times.

Hunting play: stabbing with one or both forepaws at a presumably imaginary prey or other stimulus in the grass. This was common in *Chrysocyon*, rare in *Cerdocyon*, and absent in *Speothos*.

Although nearly all of these youngsters' active social behaviours would be considered 'playful' by most observers, the interspecific differences among them, particularly those of *Speothos* from *Cerdocyon*, *Chrysocyon* and other canids, were large enough to defeat the use of an acceptably narrow definition of play. Other studies have likewise had little success in abstracting the qualities held in common in the play of different species, i.e. what makes behaviour appear playful. No broad definition of play can eliminate the possibility of recording non-play as play (Stevenson & Poole 1982). The reverse situation, failure to report the incidence of behaviours that are not obviously play, is a greater danger. What, for instance, does one do with clearly non-playful behaviours like muzzle licking or sniffing, which sometimes initiate clearly playful behaviours like muzzle-wrestling? Or, unsuccessful attempts to initiate play with a partner? I have chosen here to make no arbitrary judgments about the motivational basis of behaviours. Instead, all social interactions are considered together here, regardless of whether they appeared to the observer to be playful, affiliative or aggressive. 'Play' is retained in the naming of behavioural categories that were mainly imitative or manipulative, e.g. 'object play'.

Social interactions are here defined to include all pup behaviours directed at other pups or the parents (whether reciprocated or not), or activities engaged in by more than one individual. A sub-category, Sustained Social Interactions, is defined as interactions in which two or more participants alternately or simultaneously directed behaviours at each other. This sub-category includes, but is not limited to, behaviours commonly referred to as play. Unless otherwise stated, 'social interactions' or 'interactions' as used here includes both types.

Results

Behavioural Repertoires

All major behavioural categories listed above occurred in both *Chrysocyon* and *Cerdocyon*. Except as noted, behaviours were performed similarly by all three species, within the constraints imposed by differences in morphology. *Speothos* differed from the other two species by showing defence play, which was not seen in the other two, and lacking hunting play, grappling and bowing. Although the relatively short legs and bulky forequarters of *Speothos* at first appear to preclude the bipedal stance

used in grappling, this explanation seems unlikely, since individuals stood bipedally to sniff urine marks and other olfactory stimuli. Morphological constraints on ground-wrestling also seem unlikely.

Biting occurred in all three species and target preference differences were minimal (Fig. 1). The head and neck region received over 60% of all bites in each species. Although *Speothos* directs bites to the neck, where the skin is thicker, during fights (Kleiman 1972), the neck was not a preferred target in other

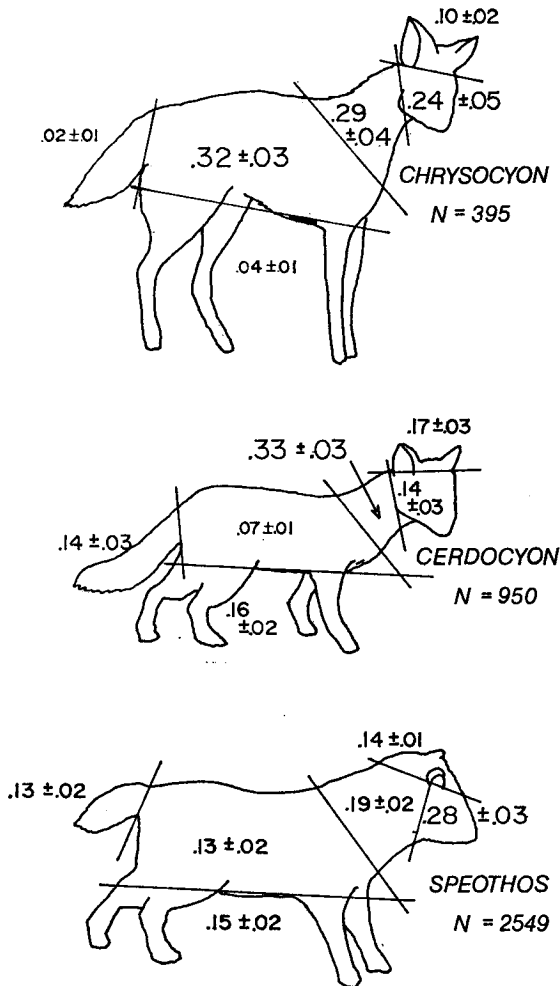


Fig. 1. Biting targets: Mean (\pm SE) percentage of bites directed to different body areas. Size of number corresponds to magnitude. N = number of bites for which target was observed. Relative size of animals is not to scale.

contexts. Shaking while biting occurred occasionally in very young pups of all three species, but was rare in older pups and was not typical in adults killing prey.

Developmental Schedules

Very early physical and social development, with the exception of eruption of the canine teeth, was comparable in all three species (Table I). Differences first appeared in the third week, when *Cerdocyon* pups began to show the social interaction behaviours that would make up the bulk of their social repertoire over the next few months. *Chrysocyon* and *Speothos* lagged about a week behind *Cerdocyon* in most of these behaviours.

Time Course of Social Interactions

The percentage of time spent in social interactions was initially very low, increasing to a peak, and then declining in all three species (Fig. 2). The peak occurred earlier in *Chrysocyon* and *Cerdocyon* (weeks 13–14) than in *Speothos* (weeks 17–18). During the eight weeks of greatest social activity for each species, *Speothos*' percentage was significantly greater ($P < 0.01$, Mann-Whitney U test) than either of the other two species (*Speothos* (weeks 13–20), $\bar{X} = 0.239 \pm 0.018$ SE, $N = 9$ with litter S3 omitted because the period of observation did not include weeks 13–20; *Chrysocyon* (weeks 11–18), $\bar{X} = 0.148 \pm 0.013$ SE, $N = 8$; *Cerdocyon* (weeks 9–16), $\bar{X} = 0.142 \pm 0.011$ SE, $N = 9$). The difference between *Chrysocyon* and *Cerdocyon* means was not significant.

Who Interacts with Whom

For all litters where pups had siblings of both sexes, the frequencies of interaction with males and females were analysed as a matched pair by the Wilcoxon test (Byers 1980). There were no significant differences (two-tailed, $\alpha = 0.05$) in (1) choice of own versus opposite sex, and (2) choice of males versus females. Neither was there any significant tendency for pups to interact with (or avoid interacting with) the parent of the same sex. *Speothos* pups of both sexes interacted most often with the male parent ($T = 1$, $N = 12$, $P < 0.01$). *Cerdocyon* pups of both sexes displayed submissive behaviour to the male parent most often ($T = 0$, $N = 9$, $P < 0.01$) but did not differentiate for other pup-parent activities, the majority of which were licking and sniffing.

Table I. Developmental Schedules

Event	Day of first occurrence in a litter		
	<i>Chrysocyon</i>	<i>Cerdocyon</i>	<i>Speothos</i>
Gestation period	62–68 days ^{1,2}	52–59 days ^{1,3}	65–76 days ¹
Eyes begin to open	7 ⁴ , 8–9 ² , 9–11 ⁵ , 10, 11 ⁶ , 13	14, 14 ³	8, 11, 12 ⁷ , 17 ⁸
Ears begin to open	8–9 ² , 9–11 ⁵ , 16	14, 14 ³	12 ⁸ , 14
Early social interactions: pawing, mouthing, licking, head-butting	8 ² , 9, 18	11, 13 ³	9, 17, 18
Canine teeth erupt	11 ⁴ , 14	13, 14–16 ³	23, 23–25 ⁸ , 25
Muzzle wrestling	21 ² , 23, 26	14, 17 ³	16, 19, 28
Biting	20, 21 ² , 24	14	19, 20, 28
Standing over	week 3 ³ , 23, 24	13 ³ , 14	20, 24, 33
Grappling	21 ² , 22, 24,	17 ³ , 22	—
Rolling over	28, 31	22	19, 21, 28
Begin eating solids	week 4 ² , 32 ⁴ , 33, 34	20 ³ , 28, 32	38, 43
Fighting	30–40 ⁵ , 39, 47	31, 33	43, 44, 49
Chasing	40, 45	27, 40	40, 49, 50
Object play	39, 40	39, 40	39, 43, 51
Raised leg urination in males	10 months ²	week 23, week 29, 5 months ³	week 14, week 16, week 18–20 ⁸

¹records of National Zoological Park.

²Brady & Ditton (1979).

³Brady (1978).

⁴Acosta (1972).

⁵Schneider et al. (1979).

⁶Haemmerling & Lippert (1975).

⁷Kitchener (1971).

⁸Drüwa (1977).

All other entries refer to litters in the present study.

Social Interaction Length

The frequency of social interactions decreased exponentially with length in all three species, conforming to the general 'logarithmic law of ecology' which predicts that animals will demonstrate most often the activities that represent the least effort, e.g. shorter activity bouts (Cherry 1966). Most interactions were short, 10 s long or less; bouts longer than 60 s represented less than 10% of the total. There were no interspecific differences.

Behaviours Occurring during Social Interactions

Differences in the frequencies of major behavioural categories were apparent among the three species (Fig. 3). *Chrysocyon* and *Cerdocyon* were most similar to one another, while *Speothos* was very different from them both. The most striking differences were the absence of GR from the repertoire of *Speothos*, and the very low incidence of VO during *Chrysocyon* and *Cerdocyon* interactions.

Some behaviours were more successful than others in initiating sustained social interactions. Those behaviours that led significantly (χ^2 , $df = 1$, $P < 0.05$) often to sustained social interactions are here referred to as 'initiators'.

In *Cerdocyon*, GA and EA acted as initiators, while in *Speothos* and *Chrysocyon*, EA and RO (to an adult or another pup) were initiators. Gaping during interactions was very common in all three species, often being performed in conjunction with other social behaviours. By itself, however, it was an initiator only in *Cerdocyon*. All initiators were non-contact: that is, they potentially signalled intent without risking actual contact.

The probable sequence of events in social interactions that began with initiator behaviours, as presented in the form of kinematic graphs (Sustare 1978), is similar for *Chrysocyon* and *Cerdocyon*; but *Speothos* is quite different (Fig. 4). To reduce complexity, only the most frequent behaviours and their major transitions are given. Those representing less than 3% of the total, by frequency of occurrence, are omitted. The *Speothos* model, although simpler than the other two, nonetheless accounts for more of the species' behaviour during interactions than do the other two (Table II). The model for *Chrysocyon* is the most complex, yet accounts for the lowest percentage of behaviours. Figure 4C is the most determinate of the three in that sequences showed the clearest one-way

progression from initiator to termination. The transitions in Figs 4A and 4B are more flexible, making a prediction of the next behaviour in a sequence more difficult.

Solitary Activity and Social Activity

Very little of the pups' behaviour could be interpreted as 'solitary play' because the activity

of one pup tended to attract the attention of others, who were rarely rebuffed. Exceptions were as follows:

- (1) Hunting play, which was quite infrequent (less than 1% of behaviours observed), was nearly always solitary in both *Chrysocyon* and *Cerdocyon*. It did not occur in *Speothos*.
- (2) Object play was usually solitary in *Chrysocyon* (52% of cases) and in *Cerdocyon* (83% of cases), but usually social in *Speothos* (77% of cases).

Although dyadic interactions were the most common in all three species, regardless of litter size, additional pups often joined in for a time.

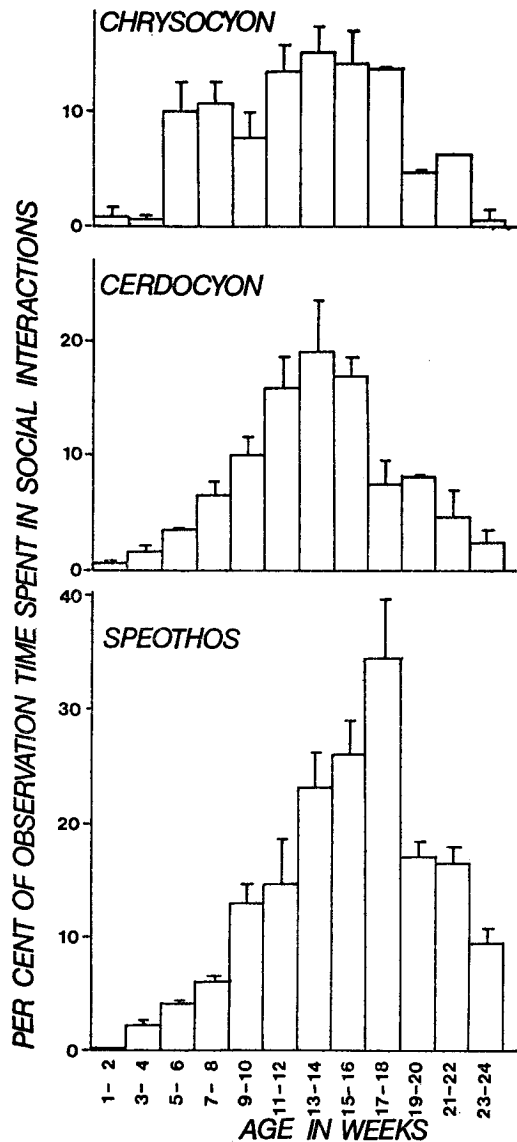


Fig. 2. Time course of social interactions, showing means \pm SE.

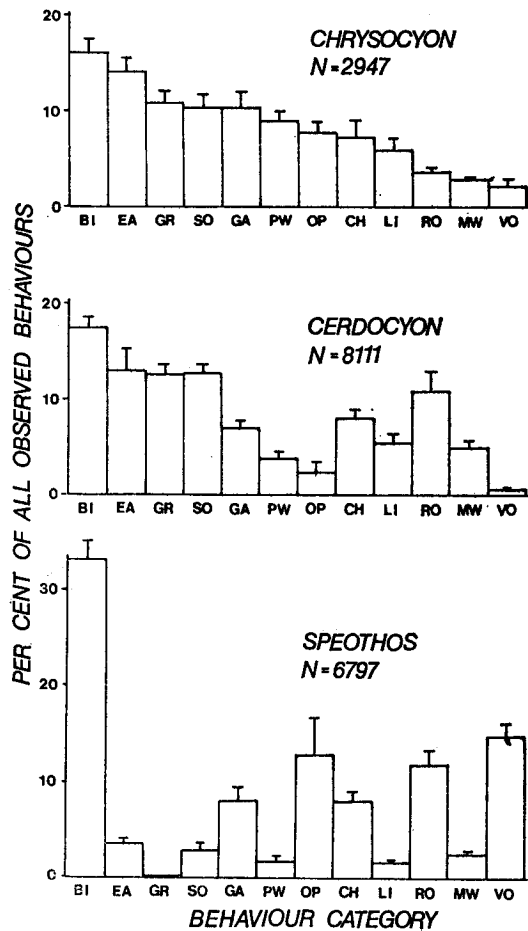


Fig. 3. Frequencies by occurrence of behaviour categories: = n of times behaviour category occurred divided by total N of behaviours. Categories are ranked on the abscissa with respect to *Chrysocyon*.

CH and GR were commonly group activities in *Chrysocyon* and *Cerdocyon*: CH, OP and BI in *Speothos*.

Ontogeny of Social Behaviours

The frequencies of several important behavioural categories (RO, SO, GR, CH and BI) maintained approximately the same relation

to each other throughout early ontogeny (Fig. 5). However, in *Chrysocyon*, SO and GR were disproportionately frequent in younger pups, CH in older pups. No significant differences (two-tailed Mann-Whitney U test, $\alpha = 0.05$) were found between the sexes, in either young (3–6 weeks) or older (15–18 weeks) pups, for any of these behaviours.

Social Relations within the Families

The usual method for determining social dominance in young canids has been through observation of fights and subsequent avoidance by subordinate animals (Fox & Clark 1971; Bekoff 1974, 1978). However, none of the brief periods of fighting that occurred in each litter had any obvious effects on the subsequent behaviour of the interactants. A second means of assessing social rankings, by stimulating competition over food (Scott & Fuller 1965; Fox 1972) was not considered a valid test here, since access to food is not normally determined by dominance in these species (Biben 1982b). The *Chrysocyon* pups did not kill live prey while housed with their parents, regardless of whether the parents were actually present. In both *Chrysocyon* and *Cerdocyon*, any pup possessing a food item defended it from all others. *Speothos* pups, in contrast, never defended a food item.

There were, in fact, no obvious indications of major differences among pups with respect to social rankings or dominance. No individual was consistently excluded from interactions or resting groups. Likewise, no pup had preferential access to food or resting sites. However, more subtle behavioural differences among the pups indicated inequalities in social status or personality. In all litters, pups showed the typical canid behaviours of standing over (SO) and rolling over (RO), which are often considered to be dominance and subordination displays (Fox & Clark 1971). 'Dominant' individuals would be ones who stood over others but were not themselves stood over. Ratios of SO performed/SO received for each individual in a litter were ranked and followed over time (Fig. 6) for *Chrysocyon* and *Cerdocyon* litters. SO frequency in *Speothos* was too low for this analysis; RO performance was used instead (Fig. 7). All litters except C1 showed very unstable rankings over time. In C1, the 'dominant' pup was a female who was considerably larger than her littermates.

Pups showed RO to both parents and other pups. In each litter, adults received more sub-

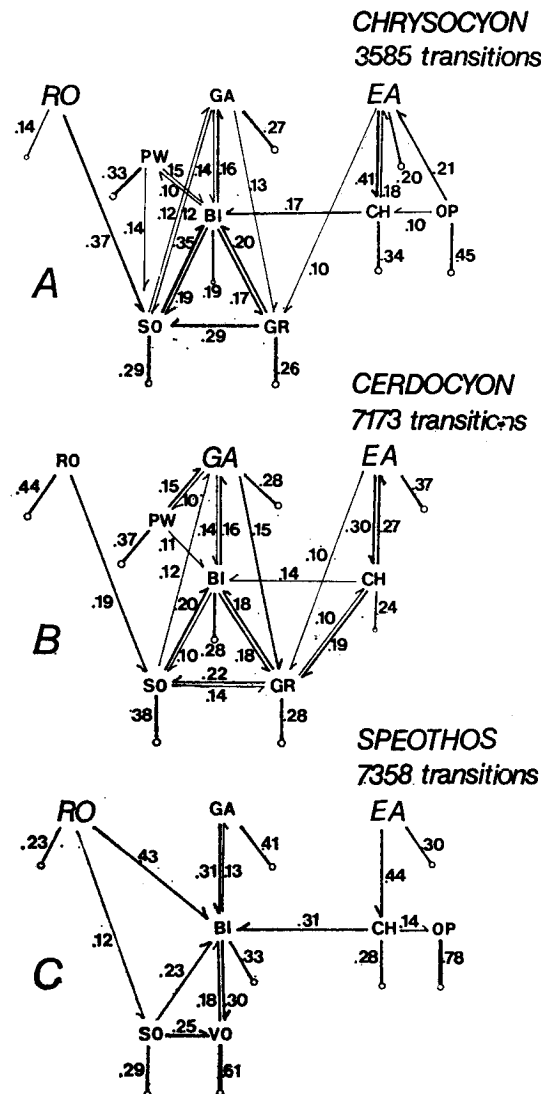


Fig. 4. Kinematic graphs of major first-order transitions. Differences in arrow thickness correspond to magnitude of transition frequency. Larger letters indicate initiator behaviours, small circles indicate end of interaction. Placement of behavioural categories (if they occur) is identical for each species.

Table II. First-order Transitions Accounted for by Fig. 4 (Frequencies of behaviour (column A) are from Fig. 3)

	Behaviour of origin	A Frequency of behaviour	B % of transitions represented	% of Total transitions represented (A × B)
<i>Chrysocyon</i>	BI	0.16	0.81	0.1296
	EA	0.14	0.71	0.0994
	GR	0.11	0.77	0.0847
	SO	0.10	0.76	0.0760
	GA	0.10	0.66	0.0660
	PW	0.09	0.62	0.0558
	OP	0.08	0.76	0.0608
	CH	0.07	0.69	0.0483
	RO	0.04	0.51	0.0204
	Totals	0.89		0.6410
<i>Cerdocyon</i>	BI	0.18	0.72	0.1296
	EA	0.14	0.77	0.1078
	SO	0.13	0.84	0.1092
	GR	0.13	0.78	0.1014
	RO	0.12	0.63	0.0756
	CH	0.09	0.84	0.0756
	GA	0.07	0.67	0.0469
	PW	0.04	0.63	0.0252
		Totals	0.90	
<i>Speothos</i>	BI	0.33	0.76	0.2508
	VO	0.15	0.79	0.1185
	OP	0.13	0.78	0.1014
	RO	0.12	0.78	0.0936
	CH	0.08	0.73	0.0584
	GA	0.08	0.72	0.0576
	SO	0.03	0.77	0.0231
	EA	0.03	0.74	0.0222
		Totals	0.95	

missive behaviour than did pups. The percentage (mean \pm SE) of pups' ROs directed to different classes of individuals was as follows: *Chrysocyon* (litter Chl only), to adult male: 0.26 ± 0.04 , to adult female: 0.31 ± 0.03 , to other pups: 0.22 ± 0.06 ; *Cerdocyon*, to adult male: 0.55 ± 0.04 , to adult female: 0.22 ± 0.03 , to other pups: 0.08 ± 0.03 ; *Speothos*, to adult male: 0.32 ± 0.04 , to adult female: 0.14 ± 0.02 , to other pups: 0.16 ± 0.02 . RO to adults occurred most often during or after grooming or sniffing by the adult or in response to the approach of an adult, particularly the male. In all three species, simultaneous ROs by several pups were directed to the adults only, never to another pup, and frequently accompanied attempts to suckle or beg food from the parents. Pups never stood over a parent.

Social distances maintained by the family group varied in the three species. *Speothos* pups rested in contact with their parents and moved as a cohesive group with them for at least 6 months. The *Chrysocyon* pups, in contrast, began resting several metres apart from each other and the parents by the end of the second month. *Cerdocyon* pups were intermediate, usually resting within a metre of each other or a parent (usually the mother).

Discussion

All behaviours reported here have been identified in other canids and, with the exception of grappling (absent in *Speothos*), all of the most commonly-occurring categories were found in each species studied here. However, the frequency of performance of these behaviours

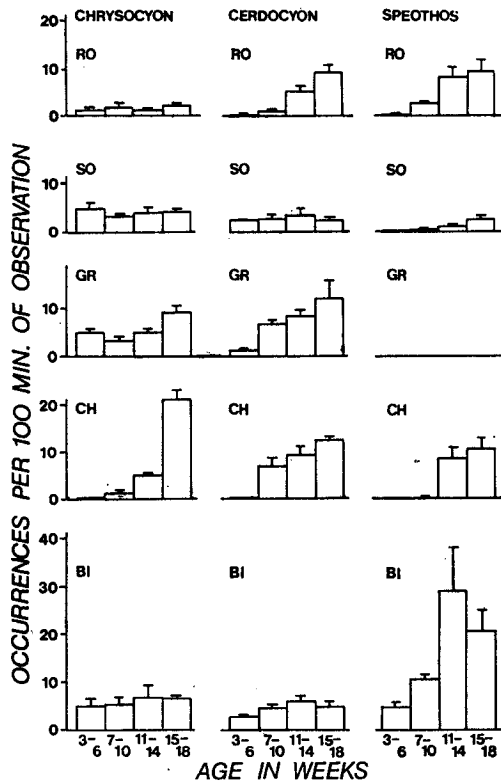


Fig. 5. Time frequencies (mean \pm SE) of behavioural categories during ontogeny.

varied widely. The emphasis on biting, vocalizing and rolling over, and the absence of grappling, made the interactions of *Speothos* appear very different (less 'playful') than those of domestic dogs and all other canids for which early social behaviour is described. *Chrysocyon* and *Cerdocyon* interactions were more *Canis*-like, featuring grappling and leaping about, as well as biting. However, juvenile 'sexual' mounting with clasping was much rarer than suggested by other canid studies (e.g. Fox 1969). The infrequency of a ritualized play bow (Bekoff 1977) in *Cerdocyon*, and its absence in *Speothos*, is also unusual for Canidae. Unritualized exaggerated approach and leaping about appeared to serve the same purpose as a play bow in these two species, initiating sustained social interactions. *Chrysocyon* showed the play bow as well as the unritualized behaviour. The open-mouth gape or play face which, like the play bow, communicates playful intentions, and is commonly displayed during friendly interactions

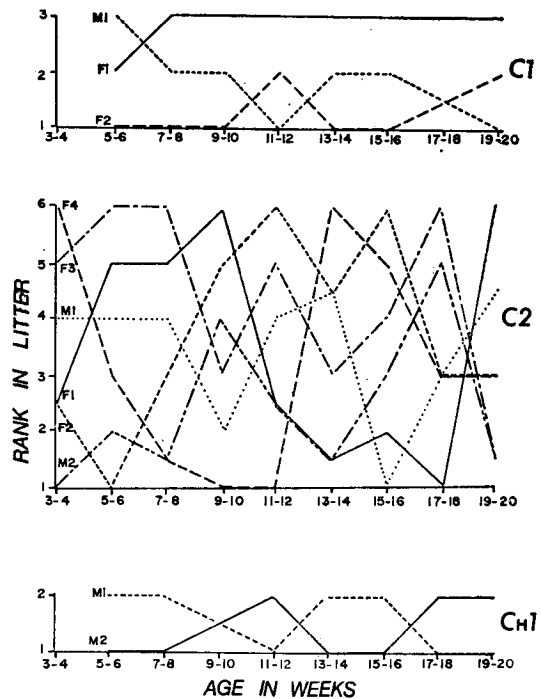


Fig. 6. Time course of rankings of SO given/SO received for *Cerdocyon* and *Chrysocyon* litters that were observed for 6 months. Litter Ch2 (not shown) was similarly unstable. M = male pup, F = female pup, 1 = lowest ratio of SO given/SO received (least 'dominant' individual).

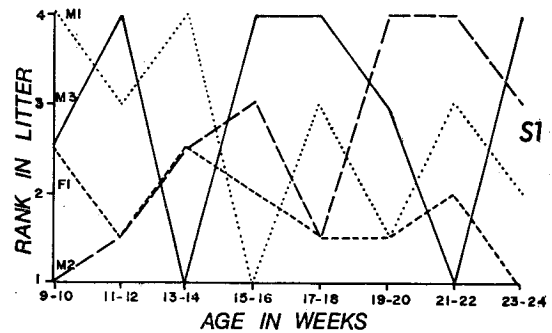


Fig. 7. Time course for rankings of RO given/RO received. M = male pup, F = female pup, 1 = lowest ratio of RO given/RO received (least 'subordinate' individual).

in wolves, coyotes, foxes (Fox 1970) and other carnivores, was used in comparable situations by the three canids studied here.

Fighting, except over possession of food in *Chrysocyon* and *Cerdocyon*, was limited to a period of a few weeks and had no profound

effect on social relations. Indeed, *Speothos* pups who fought continuously for 15 min rested in contact immediately thereafter. The occurrence of an early and limited period of fighting, like those listed in Table I, was also noted by Bekoff (1978) in coyotes, where the outcomes of fights established definitive and enduring social relations. No such correlation was identified in the present study and no explanation is here offered for the existence of a fighting phase in the development of the South American canids. Although Bekoff (1978) reported that fighting precedes play in coyotes, this was not the case for the canids in the present study.

In some highly social species, the young are reported to be highly interactive (Bekoff 1974; Happold 1976), while in others, like the collared peccary *Tayassu tajacu*, the young are non-interactive and aggressive among themselves (Byers, in press). No differences occurred here in the duration of interactions; however, *Speothos* pups did spend a greater percentage of their time interacting than did *Chrysocyon* or *Cerdocyon*. There are a number of possible explanations for this difference. *Speothos* may have a greater tendency towards social interaction. Or, the decreased social distance maintained by a social species may more frequently put individuals in a position to interact. However, since no difference in interactiveness was seen between *Chrysocyon* and *Cerdocyon*, there is little evidence here to suggest that social interactiveness of the young varies in accordance with the degree of sociality of the species. Also, dyadic (rather than group or solitary) activity was the most common type in all litters of all species, although quantification of this measure is difficult in different-sized litters. *Speothos* does show a higher frequency of group object play and is relatively non-competitive in this activity, one that appears to correlate well with group hunting and therefore with sociality (Biben 1982a).

Another possible explanation for the higher frequency, and later peak, of juvenile social interactions in *Speothos* is neotenic development. Adult *Speothos* are paedomorphic, retaining the large head, short muzzle and short legs of infancy. The motor development of pups (chasing, standing over, etc.) and progression to eating of solid foods are retarded for a carnivore of its size. Data in Table I place *Speothos* closer to the much larger (26–28 kg adult weight) *Chrysocyon* than to the comparably-sized *Cerdocyon*. Paedomorphosis by neoteny

may be related to an extended period of juvenile dependency, playfulness and learning in some social species (Gould 1977; Fagen 1981, page 256).

The data on social relations give little evidence for the existence of enduring dominance hierarchies within the litters. Even in the one litter where a dominance hierarchy was most strongly suggested (C1), the 'true' dominant animal, as evidenced by the number of rollovers received, was clearly the adult male. In all three species, only the adults received group displays of submission. Lockwood (1979) stresses subordination displays, rather than dominance displays, as the key to social relations in wolf packs.

The subtlety of dominance relations, if in fact any existed, among the pups, argues against the importance of a dominance hierarchy as a major influence on behaviour. This is not in agreement with the emphasis placed on the role of dominance in young wolves, foxes and coyotes by Fox (1969, 1972), Fox & Clark (1971), Bekoff (1974), and others. It is unlikely that the South American canids differ that much from the North American ones. More likely, the difference lies in the fact that here families were kept intact, with (except in one case) both parents present, and pups were not kept artificially isolated from one another for any period of time. It is clear that differences in weight, health or even 'personality' may influence the pups' activeness, tolerance, and aggressiveness, thus causing marked differences in behaviours like standing over. Small, sickly pups will often be subordinate, while large, heavy pups will be dominant. However, the point to be made is that it is not at all clear that the linearity, stability, or sex-specificity of a hierarchy are species-typical characteristics or are predictive of a species' social organization. It is suggested here that social relations in the intact, typically monogamous canid family are best described as follows: the mated pair is dominant over any youngsters remaining with them, with dominance relations among pups being highly variable. This appears to be true regardless of the characteristic dominance relations of the adults of the species. *C. lupus* adults have characteristic male and female dominance hierarchies, but Zimen (1976) describes young parent-raised wolves as having no established or consistent rank order. The mated pair in the South American species studied here do not have characteristic dominance

relations: either sex may be dominant and the degree of dominance is variable, often changing with the reproductive cycle (Porton, unpublished data). Thus, social relations in many canids may resemble those of many Old World primates (e.g. baboons, *Papio*: Rowell 1966, 1974), where an individual's age class and reproductive condition are most predictive of its relation to others in the group.

The behavioural categories rolling over and standing over are of special interest here. While the frequency of SO equalled or exceeded that of RO in *Chrysocyon* and *Cerdocyon*, RO predominated in *Speothos*. Rolling over is very prominent in adult *Speothos* as well. Kleiman (1972) points out the conspicuous nature of *Speothos* submissive postures and discusses their importance in reducing intraspecific aggression in a social group. Adult *Speothos*, like juveniles, initiate interactions by assuming a submissive posture (Kleiman 1972), behaviour that is also seen in the highly social *Canis lupus* (Schenkel 1967; Woolpy 1968), *Lycaon* (Estes & Goddard 1967), and *Cuon* (Johnsingh 1980). Submissive behaviour emerges early as a major behaviour in *Speothos* pups and may be instrumental in maintaining the close social distance and high degree of interactiveness characteristic of this species.

The form or sequencing of interactions was a major point of difference for the three species. *Chrysocyon* and *Cerdocyon* interactions were more complex than those of *Speothos*. That is, behaviours in the former two tended to lead, with about equal probability, to three or four different behaviours, while *Speothos* behaviours had only one or two likely outcomes. Because of this, *Speothos* interactions appeared more determinate. However, some degree of directionality was present for all three, as particular behaviours could be identified which were more likely to initiate sustained social interactions. These behaviours are referred to as 'initiators' rather than 'play invitations' or 'play solicitations' in the sense of Bekoff (1972), because it is felt here that 'invitations' implies an intent which may not be present. For instance, it is not clear that a *Speothos* pup who rolls over and is then bitten by others did so in order to be bitten, although this sequence of events was highly predictable.

The type of activity that characterized *Chrysocyon* and *Cerdocyon* interactions has been called 'play fighting', 'rough and tumble play', and 'aggressive play' in other studies and

is a typical form of mammalian play. Its function has been a controversial issue, but recent studies of instances of extreme sexual dimorphism in aggressive play have strongly indicated that it is related to adult combat skills. Play-fighting resembles unritualized adult fighting, but lacks the agonistic signals that prevent or stop 'serious' fighting—loud vocalizations, piloerection and submission (Symons 1978). Although *Chrysocyon* and *Cerdocyon* fitted the play-fighting description well, *Speothos* did not. Loud growls, whines and squeals, and rolling over with flattened ears and lips retracted in a grin were all common during *Speothos* interactions. While rolling over acted as an initiator in *Chrysocyon*, it was not sustained, and the interactants went on to other activities. This was not true for *Speothos*.

The overall lack of sex differences in these canids is in accordance with the prediction of Fagen (1981), based on a review of the literature, that carnivores will show few differences in play because, as adults, males and females have similar roles, capturing food, holding and defending territories, and defending and training youngsters. The three species studied here appear to fit this model well, having little behavioural or size dimorphism between adult males and females.

In conclusion, it is clear that the ontogeny of behaviour in the highly social *Speothos* is very different from that of the less social *Cerdocyon* and *Chrysocyon*, and from the well-studied *Canis* species. Points of difference did not follow conventional ideas about the ways in which sociality is likely to develop, e.g. that the young of more social species will show more complex behaviour, be less aggressive, and have a well-defined dominance hierarchy. *Speothos* pups expressed a less rich and varied repertoire during interactions and showed a higher frequency of behaviours considered to be aggressive (e.g. biting, growling). Although both aggressive and submissive behaviours were prominent, *Speothos* showed no stable social hierarchy of dominance relations. They interacted more often but bouts were not longer. *Chrysocyon* and *Cerdocyon* emphasized in their interactions alternating among grappling, chasing, standing over, and biting—behaviour apparently serving to prepare for intraspecific combat. *Speothos*, in contrast, lacked grappling and concentrated on what were essentially displays of submission to the group—behaviour that was reinforced

or intensified through repeated biting of the submissive pup by the littermates.

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