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Degree of Behavioral Neoteny Differentiates Canid Polymorphs

By R. Coppinger, J. Glendinning, E. Torop,
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Abstract

As with juvenile wolves or coyotes, adult livestock conducting dogs displayed the first-half segment of a functional predatory system of motor patterns and did not express play or social bonding toward sheep; whereas, like wolf or coyote pups, adult livestock protecting dogs displayed sequences of mixed social, submissive, play and investigatory motor patterns and rarely expressed during ontogeny (even when fully adult) predatory behaviors. The most parsimonious explanation of our findings is that behavioral differences in the two types of livestock dogs are a case of selected differential retardation (neoteny) of ancestral motor pattern development.

The “neotenization hypothesis” (Geist 1971) suggested a correlation between morphology and behavior in clinal members of *Ovis*, among which the most northern and recent forms had been selected for larger horn size, which GEIST argued was the result of selection for a longer growth period (i.e., a retardation of the onset of adult characteristics). Geist hypothesized that forms that showed morphological neotenization would also show evidence of behavioral neoteny. We use the term “neoteny” as Kollman (1885) defined it originally and as Gould (1977, pp. 227–229) has recently redefined it: a retardation of development leading to the retention of ancestral juvenile or embryonic characters. Often neoteny results in the retention in the adult offspring of not just one but a number of organ systems—a whole package—of ancestral juvenile morphological and behavioral characters. A corollary of the process of neoteny is that the same retardation of development that results in retention of juvenile characters in the neotenic descendant must also attenuate or render vestigial ancestral adult characters (de Beer 1930, pp. 37–38, 75; Gould 1977 p. 228).

Many authors (Lorenz 1952; Zeuner 1963; Ratner & Boice 1975) have suggested that dogs (*Canis familiaris*) are the neotenic descendants of an ancestral form. See Price (1984) for a review of neotenic behavior in domesticated animals. Fox (1965, 1978), following Dechambre (1949), suggested differential neoteny or

selected retardation as a possible mechanism for the polymorphic behavior of the different breeds.

The difficulties in testing the neotenization hypothesis with dogs are numerous. Perhaps the most severe limitation is that the many breeds of dogs have been selected to respond to different objects in a wide range of habitats, which makes adequate control of a comparative experiment difficult. In addition, since there is a long maturation period and a large behavioral variance, the time and expense of raising a large number of animals under controlled conditions has been practically impossible. Yet working dogs present a unique opportunity to study the evolution of polymorphic behavior, for they are probably the only mammals for which we have clear statements of the behavioral differences that were under selection.

Within the category of working sheepdogs exist two distinct types, markedly different in both morphology and behavior, yet both selected to respond to identical stimuli, primarily sheep (*Ovis aries*). The functional difference between the two types is that Conducting Dogs (Herding Dogs) move livestock from place to place, disrupting the sheep's behavior, while Protecting Dogs (Guarding Dogs)¹ are expected to be attentive to sheep and non-disruptive to their behavior while entering into agonistic displays with potential predators (COPPINGER & COPPINGER 1982). These two types have been bred for many generations in separate but environmentally similar grassland habitats (generally, Conducting Dogs in Great Britain and Protecting Dogs in Eurasia) to exhibit very different motor patterns toward sheep, thereby providing an exceptional opportunity for experiments comparing these behavioral polymorphisms.

Some breeders of Conducting Dogs assume that their eye, stalk, and chase behaviors are predatory homologues (Holmes 1966; Vines 1981; McConnell & Bayliss 1985). Coppinger & Coppinger (1982) postulated that Protecting Dog behavior was an extremely retarded canine development whereby shepherds had selected individuals that did not show the onset of predatory motor patterns. They further postulated that the resulting animals would show a high frequency of infantile and early juvenile motor patterns and would not show predatory patterns to potential prey. Fox (1978), Ginsburg & Schotte (1978), and Frank & Frank (1982) found similar neotenization of motor patterns in several breeds of dogs compared to wild Canis. Furthermore, it was hypothesized that juvenilized animals lack species-specific social bonding patterns, the lack of which may enable attachment or attentiveness to other species. of dogs compared to wild Canis. Furthermore, it was hypothesized that juvenilized animals lack species-

¹ The literature on "Shepherd" dogs and "Guard" dogs is not clear as to functional behavior. For example, German Shepherds are bred neither to protect nor to herd sheep in the same way as other "Shepherd" dogs, and the popular literature refers to Dobermans as "Guard" or "Guarding" dogs. Europeans use the term "Conducting" dog to differentiate a herder, or shepherd's dog, from a shepherd dog that is a guarding dog. We have chosen the terms Protecting (following Black & Green 1985) and Conducting as descriptive and least confusing.

specific social bonding patterns, the lack of which may enable attachment or attentiveness to other species.

Behaviors that tend to characterize and distinguish different breeds of dogs have been studied in some detail by behavioral researchers. These studies have tended to focus on comparative psychological responses to various environmental stimuli (Mahut 1958; Scott & Fuller 1965), hereditary differences in trainability (Fuller 1955; Elliot & Scott 1961), or psychological differences as a consequence of developmental differences (Freedman 1957). The present investigation focuses on behaviorally different livestock-working breeds that have been selected to respond to the same-environmental stimulus (i.e., livestock) with different motor patterns and, in particular, with different organizations of motor patterns.

Our general premise is that during ontogeny and subsequently when adult, polymorphs selectively retarded at different ontogenetic stages of the ancestral stock would continue to display systems of behavior corresponding to different stages of the ancestral behavioral ontogeny. Moreover, conducting and protecting dogs would continue to display their different systems of behavior regardless of the response, species or size of the animals with which they interact. We investigated several breeds of livestock protecting dogs and one breed of livestock conducting dogs to see whether the quality and frequency of their behavior differ in ways that correspond to different stages of the behavioral development of the wild type that we presume to be ancestral.

Methods

The Study Animals

The Livestock Conducting Dog (CD) breeds, highly developed to herd livestock, are found mainly in Great Britain (collies), with derivatives in Australia, New Zealand and North America. Generally, conductors are divided into two groups: “heelers” that chase and bite the heels of large livestock (e.g., cattle), and “headers” that circle around fleeing sheep, or sometimes cattle, and head them off. Conducting dogs tend to be small, 12–20 kg (Vines 1981).

Within livestock conducting breeds, the quality and the frequency of display of specific motor patterns is remarkably consistent. Between conducting breeds, behavioral specialties such as heading, heeling, voicing, or posturing can be seen. Training enables the shepherd to control, direct and inhibit the dog’s behavior, provided the necessary motor patterns have been expressed. A conducting dog cannot be taught to work with livestock until it exhibits conducting behaviors at some point in its ontogeny. A Border collie, for example, exhibits little or no directed interest in livestock until it develops “eye” (Holmes 1966). Even though

breed training literature (Free 1949; Wehle 1964; Holmes 1966) points to considerable variation within breeds in the onset times, during development, for specific motor patterns, such well defined onsets (sooner or later) suggest that these behaviors are under some genetic, as well as environmental, control.

The Livestock Protecting Dog (PD), although relatively rare, is locally common in the Mediterranean, eastern Europe, Asia Minor and Asia, with derivatives in South America, areas where domestic sheep, goats and predators exist sympatrically. Regionally, these dogs are distinct in superficial characteristics such as hair length and color, while in gross morphology and behavior they tend to be similar. They weigh 30–45 kg. As with conducting dogs, livestock protecting dogs display their characteristic behavior patterns without much formal training. Several popular hypotheses exist about procedures required for socializing future protecting dogs with target livestock (Darwin 1845; Arons 1980; Green & Woodruff 1983; or training them to protect against coyotes, Linhart et al. 1979), but whatever environmental conditioning is necessary has not yet been demonstrated. Protecting dogs do not conduct livestock, nor are they encouraged to. Rather, their value may be measured in terms of the degree to which they 1) do not disrupt livestock activity (trustworthiness), 2) maintain an orientation to livestock (attentiveness) and 3) prevent livestock from falling prey to other carnivores (protectiveness) (Coppinger and Coppinger, 1980; Coppinger, et al, 1983b).

Between 1977 and 1980, livestock dogs were collected from various sources of working stock. 32 dogs were purchased in Europe and Asia Minor from active sheep farms and collectives and 29 were donated by U.S. breeders. The population of PDs used in these experiments consisted of four breeds that were either original stock or the F₁ generation stock of dogs imported from Yugoslavia, Italy, Turkey, and Portugal. Their breed names, in respective order, are Shar Planinetz, Maremma, Anatolian Shepherd and Castro Laboreiro. The population of CDs was represented by one breed, the Border collie, 6 of which were purchased from competition trial stock from Scotland. The offspring of these 6, and 7 more active working adults borrowed from farmers, were used.

Dogs were raised at Hampshire College's New England Farm Center or at the senior author's nearby farm. When they were about a year old they were bred. About 400 puppies from the livestock protecting breeds were placed on about 260 farms as part of a large-scale trial to evaluate their ability to protect livestock in the United States (Coppinger, et al. 1983 a). Individual farmers raised, maintained and put their dogs with sheep. The progress of all dogs was monitored by means of annual data reports or on-site visits.

In addition, two timber wolves (*Canis lupus*; 1 male, 1 female) and one western coyote (*Canis latrans*; male) were used in the last experiment. All three of these canids were raised in captivity and were naive to live prey.

Housing and Rearing

Ideally, conducting and protecting dogs should be raised for all experiments in the same pens, and this was done with puppies while establishing an ethogram with which to differentiate their behaviors. However, in several experiments, which are not reported here, we tried raising conducting dogs and protecting dogs together with sheep. These early experiments were invariably disruptive and were terminated. Border collies would eye, stalk and chase sheep constantly. These displays provoked aggressive encounters from the protecting dogs directed against the conducting dogs. Some experiments were conducted with dogs penned individually or in groups beside the sheep, but here again conducting dogs showed characteristic eye, stalk and chase within their pens directed at the sheep while livestock protecting dogs threatened the conducting dogs.

In the field, Border collies are usually separated from sheep when unsupervised, whereas livestock protecting dogs are expected to remain with sheep constantly, with or without supervision. We finally decided it was best to house the dogs in their normal working environment with this exception: the untrustworthy livestock protecting dogs (those that disrupted sheep) were separated from sheep unless they were supervised.

Study 1: Establishing a Partial Ethogram to Differentiate Behavioral Polymorphisms in Two Types of Dogs

Would CDs and PDs respond to the same stimuli in the same environment in different ways—i.e., does a true behavioral polymorphism exist? The argument by Black (1981) is that behavioral differences between breeds of dogs are primarily environmental. Other authors (Freedman 1957; Mahut 1958; Scott & Fuller 1965) have argued that there are not only constitutional but dispositional differences between breeds, while McConnell & Bayliss (1985) argue that the Border collie and its derivatives are the only breeds that consistently show eye and stalk motor patterns implying a different genetic repertoire. We decided to raise the two types of dogs together in the same pens and observe their behaviors. We then tested each dog individually with sheep. Our hypothesis was that between the two types of livestock dogs behavioral differences would emerge spontaneously during ontogeny, and that in spite of the fact that puppies were raised in the same environment without sheep, their first approach to sheep would be breed-typical,

In sheep communities in Mediterranean countries PDs do essentially the same work and there are no clear genetic barriers between breeds of PDs. For this reason we decided to lump all the breeds of protecting dogs into a single category of PD.

Methods and Materials

Fourteen dogs were purchased in spring, 1977: 6 CDs, 3 males and 3 females (all Border collies)² and 8 sheep protecting dogs of three breeds, 2 males and 6 females, that we lumped together as PDs. 8 PDs and 4 CDs were born on Apr. 15, 1977, and 2 CDs were born in mid-June of the same year. They were flown to the U.S. in July, 1977 and all placed in a single 20 x 30-m pen where they remained until 9 and 11 months old. The one exception is that the two youngest Border collies had to be removed when they were four months old to an adjacent 4 X 18-m pen for their own protection.

Using Altmann's (1962) ethogram of rhesus monkeys as a model, an observer, beginning in Sep. when pups were 6 and 8 months old, spent three 2-hour periods a week recording sequences of behavior until motor patterns were identified, described and catalogued in an ethogram. Efforts were taken to make this ethogram as comprehensive as possible, combining our records with the many records of *Canis* behaviors available in the literature (FOX 1969, 1970, 1971; Bekoff 1972, 1974). In Oct. 1977, when pups were 7 and 9 months old until they were 9 and 11 months old, two trained observers studied each group for a 90-minute period once a week for four consecutive weeks. Both observers were present throughout each 90-min. period. Their task was to use the complete ethogram of *Canis* motor patterns as a check list for all behaviors displayed in order to discover any and all specific motor patterns that might serve to differentiate these breeds. For we wished in subsequent experiments to focus on only those parts of the ethogram that were distinguishing. Each week, after completing their check sheet, observers wrote a narrative account of behaviors displayed in the pens. Since the observers did not yet know what specific behaviors they needed to look for, no attempt was made at this time to record frequencies, except in a narrative manner.

Two new pens were then built on either side of a sheep enclosure (9 X 9 m) in which 6 ewes were placed. After 19 days of exposure to sheep in adjacent pens, each juvenile dog, from both groups, was walked individually among the sheep on a leash in order to prevent damage to sheep. Two observers separately recorded the behavior of each dog toward the sheep. A few days later another trial was run in which dogs were exposed for 5 minutes among the sheep. This same type of 5-min. trial was repeated again one week later. The intent of these experiments was to provide observers with enough comparative data to frame and test a partial ethogram of their motor patterns that might best serve to differentiate behavior of the two morphs.

² *We restricted this study to BCs because they are the commonest trial dog, working stock was readily available, and there is a literature on the Border collie (see McConnell & Bayliss 1985).*

The observed behaviors of all puppies within each type were qualitatively similar. There was, however, a clear contrast between CD and PD, noted in the differential expression of social play, and motor patterns such as eye and stalk.

All PDs played together frequently and in general stayed close to each other throughout the observation periods. They engaged in frequent play-chase often culminating in a wrestling bout. PD wrestling, which included scruff-biting, hip-slamming and play-biting, appeared to push or pull the conspecific. Jaw-sparring, play-bows and successive leaps were also frequent. During wrestling bouts there were behavior sequences in which dominance and submissive behaviors of previously established hierarchies were reversed.

In sharp contrast to PDs, CDs rarely, during this period, engaged in social play. They spent the majority of their time eyeing and stalking real or imaginary objects or each other. As observed with PDs, behavioral variation existed. The youngest female was persistently preoccupied with a stereotypic sequence of behaviors repeated more than 10 times: eye — foreleg-stab — eye — foreleg-stab (see Ethogram for behavior definitions). Male Border collies in the adjacent pen spent the majority of their time showing eye to this female's activity. Female Border collies when attempting the eye behavior were threatened and driven off by the males.

PDs were never observed to express eye or stalk during this period and ignored the constant eyeing and stalking of the Border collies, while the Border collies eyed and stalked but rarely engaged in social play. PDs were stimulated to social play by the play of others, while CDs ignored play in PDs and were stimulated only by the eye and stalk of other CDs.

Five out of six CDs displayed clear patterns of eye/stalk/chase/ (and sometimes bite) toward sheep in their initial contacts. Even while this persistent eye, stalk, chase, and occasional bite behavior continued on the part of young Border collies, 7 out of the 8 livestock protecting dogs showed little orientation toward the sheep, although one young PD did chase a sheep. Except for this one incident, which may have been a case of play-chase, none of the PDs were ever observed to display eye, stalk, chase or bite behavior toward the sheep. The young PDs investigated the area, ignoring sheep.

Since certain motor patterns were seen to be more significant than others in differentiating behavior of livestock dog types, these preliminary observations suggested that the following partial ethogram would serve to discriminate between the two polymorphs, and further testing of these behaviors was planned.

A Partial Ethogram

Those familiar with PDs and CDs acknowledge behavioral differences, but inter-breed investigations of differences in motor patterns of these two polymorphs are established in the literature, although McConnell & Bayliss

(1985) compare several breeds of CDs. A catalogue—a partial ethogram (Lorenz 1966; Eibl-Eibesfeldt 1970; Hutt & Hutt 1970) -- of discrete units of behavior were defined in order to make possible operational comparison of the two polymorphs.

Approaches to Another Animal

Dominance Approach.: Dog moves toward Animal(s) with ears erect, tail high and steady, head high, standing tall, usually in a stiff walk not always on direct line but as if leading with one shoulder.

Investigatory Approach: Dog directs a steady but not hurried movement toward an animal(s) with ears flat, tail low or midway, head slightly above dorsal line (sometimes cocked), often preceded by an alert look.

Play Approach: Dog approaches animal(s), usually fast, in a series of jerky motions, head held high with nose tipped down, ears (which are hanging in PDs and pricked, semipricked in CDs) are oriented forward, tail wagging.

Predatory Approach (Sometimes called eye/stalk): 1) Eye. Dog crouches, often with its elbows and rear pasterns practically on the ground, or tipped with the nose oriented toward sheep. Eyes often appear glazed as if the animal was in a trance. The tail is often down, motionless, or occasionally waving slowly. Ears are directed forward and are pricked if anatomically possible. Animal is tense. 2) Stalk. Displaying this eye posture, animal stalks or creeps forward toward target. Eye and stalk almost always go together. If the target animal runs, the stalk is often accelerated forward into a predatory-chase.

Submissive Approach: Dog moves toward animal with ears flat and back, tail down or under legs, head held low and maybe off to the side, and often tipped, which tends to curve the spine, tucking the hind end in an awkward slow walk.

Behaviors Subsequent to Approach

Dominance Behavior: Dog stands over or alongside animal(s) in a posture similar to that exhibited during dominance approach.

Investigatory Behavior: Dog sniffs or licks any part of another animal in a Posture similar to that exhibited during an investigatory approach.

Play Behavior: Combination of play approach, play-bow, or play-solicit, play-chase, play-bite and paw following Bekoff's (1972) classification. We believe that play may be a conglomerate behavior composed of motor patterns from disparate functional contexts driven by perhaps several different motivations. However, play may be defined by ethologists in the future, it is an important behavior for our present investigation, because whatever play is we observe it more frequently when mammals are young

than when they are adult (Fagen 1981).

Predatory Behavior: Consecutive combinations of two or more elements of the following motor pattern sequence: eye, stalk, chase, crush-bite, dissect, ingest prey or prey-like objects.

Submissive Behavior: Dog crouches or rolls alongside animal(s) or runs or walks away from them in posture similar to that exhibited during submissive approach.

Bites

Crush-Bite. Dog crushes portion of animal with single bite; this usually results in death of the prey (Fox 1978).

Grab-Bite. Dog directs a bite at a specific part (see heading and heeling) as a result of a chase and/or capture, often combined with a foot-stab.

Jaw-Sparring. Mutual mouthing (by two or more animals) of face and neck, sometimes accompanied by vocalization and mock fighting.

Mouthing. Dog chews lightly on portion of animal; dog's teeth do not usually puncture the animal's skin.

Play-Bite. Bite immediately preceded by play-chase or play approach but not anatomically specific such as at heels or throat. Often the bite appears to be an attempt to hold the other animal or circumvent its flight. Does not appear to be predatory.

Predatory-Bite. "Follows a predatory-chase or a predatory-approach and is usually directed specifically at heels or throat.

Scruff-Bite. While in upright posture with head pointed down, dog grabs and mouths the back of another animal's neck (can be directed at conspecifics or at sheep who are treated as such).

Chases

Play-Chase. Chasing other animal(s) with ears up or forward, tail wagging, head high or straight. Bounding and chasing often not directed at animal but rather displayed in a run with a target animal. Sometimes followed by a Play-Bite or other contact but often not even eye contact is made.

Predatory-Chase. Rapid forward motion of the stalk.

Other Motor Patterns

Dissect. Dog pins down animal with forelimb(s) and rips off pieces of flesh.

Eating Behaviors. Combination of dissect and ingest.

Fore-Foot Stab. “Straight-arm” forelimb motion often used to pin down small prey (Fox 1978). Often directed to imaginary objects as vacuum activity.

Foreleg Clasp. Mounts another animal, usually but not always from the rear, and holds the animal with its front legs. May be .sexually or dominantly motivated.

Heading. Heads off fleeing animal(s) by circling around them and dropping into eye posture. Heading chases, if uncontrolled, will lead to a grab-bite directed at a sheep’s face or throat.

Head-Shake. Dog shakes animal vigorously in a lateral motion. Usually part of a grab-bite, but can also be a component of play.

Heeling. Chasing close to the rear of the animal, often biting at the hocks of the fleeing animal. Dogs that naturally heel are very hard to train to heacl.

Hip-Slam. Dog running beside another animal hits that animal with hip (can be directed conspecifically or interspecifically).

Ingest. Dog eats portion of animal.

Paw. Dog taps animal with front paw in posture similar to that exhibited during play-chase.

Play-Bow or Play-Solicit. Front legs extended, \forward and parallel to ground, rump in air, tail wagging, head pointed upward.

Terminating Interaction. Dog breaks contact by shifting orientation away from animal(s) for over 3 s.

Wrestling Bout. Mock fighting that may include jaw-sparring, scruff-biting, hip-slamming and alternately standing over, pushing or pulling and rolling over with another animal.

Study 2: Testing for Behavioral Polymorphism

Methods and Materials

In order to test our partial ethogram and its ability to differentiate behavioral polymorphisms, 19 adult PDs and 4 adult CDs were recalled from farms to compare their behaviors. PDs were divided into 2 subgroups based on livestock-directed behavior they had demonstrated on farms. 10 that had actually injured and sometimes killed sheep were placed in a subgroup called “untrustworthy” livestock protecting dogs (UPD) while others had behaved on farms as “expected” and were called “trustworthy” (TPD). We divided PDs into these 2 subgroups in order to test for qualitative behavioral polymorphisms (variation) within type as well as between PD and CD.

The frequencies of the previously defined motor patterns that were displayed by each type of livestock dog (CD and TPD, UPD) toward sheep were recorded. In all cases the dogs were exposed individually to sheep. For humane reasons different systems had to be used to measure the interactions, of both types of dogs with sheep. TPDs, for example, reacted to sheep at a very slow rate, so 16–34 h of observation were needed to get an adequate sample size. The purpose was to observe an interaction of an individual dog with sheep. Sometimes the observer might spend 30–40 h before an adequate sample size was obtained, as often happened with TPDs. UPDs and CDs, however, react much faster with sheep.

The one-zero sampling method outlined and criticized by ALTMANN (1974) was used to record the motor patterns exhibited by each TPD and CD toward sheep. Each h was divided into 60 one-min intervals that were indicated to the observers on a prerecorded tape. This sampling method provided for each dog the number of intervals during which any of the specific motor patterns contained in the ethogram were exhibited. CDs were tested using the same system. The purpose was to observe an interaction of an individual dog with sheep. However, CDs were placed with sheep at the beginning of each observation and removed at the end.

Originally, we intended to compare the data between the “expected” behavior of CDs and “expected” behavior of PDs. However, it was not until the end of the previous study that we realized that we had to account for the “unexpected” behavior of UPDs. In this new situation, we found the one-zero sampling technique to be inadequate and unacceptable because the UPDs could not humanely be left with sheep continuously in the way that TPDs are customarily left uninterrupted among sheep without supervision. We therefore turned to the narrative sequence sampling technique of Altmann (1974) to record all interactions between UPD and sheep. This allowed us qualitatively to compare the behavior of the three groups of dogs, even though the frequency and duration of behaviors between groups was, unfortunately, not strictly comparable.

A sampling period began when the dog approached a sheep or when a sheep approached the dog. The behavioral motor components of each dog/sheep interaction were recorded sequentially throughout the sampling period until the dog shifted its orientation from the sheep for over 3 s, at which time the sampling period was terminated. The next sampling period began with the onset of another dog/sheep interaction. This system was continued throughout each h-long observation. As a result, data for each dog are a set of ordered behavioral interaction patterns between that dog and sheep. Of the many reactions sheep could show to dogs, the data for only the most controlling 2 responses (stand or run away) were sufficient for analysis.

Table 1: Frequency of different approaches made to sheep by Trustworthy Protecting Dogs (TPD; N = 9), Untrustworthy Protecting Dogs (UPD; N = 10) and Conducting Dogs (CD; N = 4), in row %

Type of dog	Play	Submiss.	Dominance	Invest.	Eye/Stalk	Total No. of approaches
TPD	22	<i>41</i>	<i>4</i>	33	0	251
UPD	<i>48</i>	8	10	30	3	1892
CD	0	0	0	0	<i>100</i>	247

Italics indicate that row % is > 15.

Data on dog/sheep interactions were analyzed by computing conditional relationships in the behaviors between dogs and sheep. The goal of this statistical analysis was to identify and compare conditional probabilities in the organization of behavior, taking into account the usual difficulties of chance variability. Because we were using transitional probabilities as a descriptive tool rather than for computing Markovian analyses, our data did not satisfy rigorously the requirement of stationarity (Bekoff 1977).

Results

Analysis of data revealed that, in most instances, dogs within a group (e.g., UPD) exhibited both qualitatively and quantitatively similar motor patterns toward sheep. Even though frequency counts of each motor pattern varied slightly between dogs, proportional relationships between frequency counts of each motor pattern tended to be homogeneous (e.g., play approaches constituted about 45 % of the total number of approaches made to sheep by each UPD). Consequently, for ease of statistical analysis, all UPDs, TPDs and CDs were treated together as separate groups rather than as individual animals. The only category in which intra-group variability occurred was that of predatory behavior. 7 PDs exhibited what the observer judged to be one or more eye or stalk motor components in their behavior, whereas 13 exhibited no predatory components whatever. Nevertheless, the frequency of expression of these predatory components was so low among both TPDs and UPDs that did exhibit any, that behavioral homogeneity was assumed.

Table 1 shows the frequencies of various approaches made to sheep by the three groups of dogs. TPDs exhibited submissive approaches significantly more often ($p < .05$) than play approaches, while the opposite was true of UPDs that exhibited playful approaches significantly more often ($p < .01$) than submissive approaches. (The p values presented here were calculated using the Wilcoxon matched pairs signed-rank test [Siegel 1956] after comparing approaches made within each group of dogs, since between-group comparisons were not possible because of methodological differences.) In contrast, CDs exhibited neither play nor submissive approaches to sheep. Of their approaches, 100 % were predatory. In three Border collies, eye/stalk terminated the approach in 83 % of the encounters, while in

one CD eye/stalk was followed by a predatory-chase pattern in 81 % of the encounters. Aside from this difference, behavior directed toward sheep by the four CDs was virtually identical.

Table 2: Behavior exhibited to sheep by Untrustworthy Protecting Dogs (N = 10) following an initial behavioral interaction, in row %. The initial behavioral interaction is composed of a dog's approach and response by sheep to that approach.

Dog's initial approach	Subsequent dog behavior (in row %)						Totals
	Play	Invest.	dom.	sub.	pred.	Terminate interaction	
No response by sheep							
Play	42	41	2	5	0	10	245
Investigatory	0	96	0	1	0	2	416
Submissive	7	15	0	57	0	21	142
Predatory	34	13	0	0	26	26	38
Dominance	8	76	13	1	1	2	127
Sheep run away							
Play	76	4	0	1	1	18	454
Investigatory	32	22	0	5	0	41	41
Submissive	100	0	0	0	0	0	1
Predatory	36	5	0	0	21	37	19
Dominance	25	6	0	0	0	69	16

Italics indicate that row % is > 15 or that the total number of initial behavioral interactions is > 2

Table 2 shows the behaviors that UPDs exhibited toward sheep following the initial behavioral interaction, and includes the dog's initial approach and the sheep's response to that approach. Moreover, play, investigatory, and "termination of interaction" are the only behaviors reported in the "subsequent behavior directed at sheep" category, because submissive, predatory and dominance behaviors were so rarely exhibited.

Discussion

Within the observational limits of this experiment, marked qualitative behavioral differences were again evident between PDs and CDs. Although it is not "impossible" for a given dog to show a particular type of approach, what the evidence does show is a high probability that the two types of working sheepdog (PDs and CDs) will display qualitatively different systems of behavior. Border collies (CD) showed predominantly classic segments of the wild type predatory

sequence. However, Table 1 shows that predatory motor patterns comprised no more than 3 % of UPD or TPD approaches. Neither UPDs nor TPDs showed any tendency to follow their rare eye or stalk motor patterns with subsequent predatory behavior.

Most importantly, the behavior of UPDs was not intermediate between TPDs and CDs, as might have been supposed, but rather UPDs behaved in a manner qualitatively similar to TPDs. UPDs differed quantitatively from TPDs with a higher frequency of play and investigatory approach patterns. In UPD chases of sheep that we observed, the motivation did not seem to be predation and when a sheep stopped because of over-heating or injuring itself on an obstruction, the dog would search for a new playmate. It became clear to us that what had happened on the farms was that some sheep had been, literally, played to death by UPDs. It also became clear that by fleeing, sheep were inadvertently eliciting the UPD's increased level of play activity.

The strong conditional relationships that exist between types of approach and the dog's subsequent behavior differ when response of the sheep is considered. When sheep showed "no response" to the dog's approach, equal percentages of play and investigatory behaviors were exhibited following play approaches, and a very high percentage of investigatory approaches were followed by investigatory behaviors. Few submissive approaches were followed by submissive behavior; and a large percentage of dominance approaches were followed by investigatory behavior.

However, when sheep "ran away" from the dog's approach, a very different pattern of subsequent dog response occurred. The percentage of play behaviors increased dramatically following play, investigatory, predatory (eye/stalk) and dominance approaches. The percentage of investigatory behaviors decreased substantially following investigatory and dominance approaches. And the percentage of terminated interactions increased significantly following investigatory, predatory (eye/stalk), or dominance approaches. The particular behavior displayed by an active sheep to the approach of a UPD did not induce subsequent predatory behavior. UPDs were apparently untrustworthy not because they were more predatory than TPDs but primarily because they played with sheep the way they had played with conspecifics.

Study 3: Could Lack of Predatory Behavior in PDs be a Threshold Effect?

Some questions remained as we studied the results of this and the preceding tests. Could a larger number of predatory sequences be induced in UPDs by using small or novel prey? Our hypothesis for this experiment was that another stimulus, one even more likely than a sheep to elicit predatory behavior, should (if

PDs represent a behavioral homologue of a pre-predatory ontogenetic stage of canine behavior) still fail to elicit a predatory sequence. Such a stimulus would be likely to alter only the frequency, or duration, but not the quality of livestock dog behavior. Chickens were used because they are smaller, more inviting prey, more uniform in size, and easily alarmed into responding excitedly. Since a fleeing response in sheep changed the frequency of subsequent dog behavior, would a manipulated fleeing response in chickens produce the same or new effects? For comparative purposes, 2 cage-reared wolves (*Canis lupus*) and 1 cage-reared coyote (*Canis latrans*) that had never killed before were tested along with the dogs.

Methods and Materials

The following (1 to 4 year old) dogs (from a variety of rearing conditions) were used in this experiment: 12 TPDs, 14 UPDs, 10 CDs (Border collies), 2 timber wolves, and 1 western coyote. The experimental animals were not fed for 14 h (4--1 h) before the experiment began. White leghorn chickens were raised from chicks, chosen because their plumage was uniformly white. Ages of chickens during experimentation ranged from 9 to 15 weeks. Observations were made in a 7 X 17 m enclosure, by one observer. Before a dog was exposed individually to an unprotected chicken, it was exposed to a chicken enclosed in a 70 x 130 x 100 cm wire cage for 20 min. The cage protected the chicken but permitted the dog to become familiar with the procedure. Following these initial exposure periods with the caged chicken, each dog was exposed to an unprotected chicken for two 20-min periods in the enclosure.

Since our previous experiment showed that sheep were less likely to be harmed if they did not flee from a dog, one of the exposure periods was carried out with a chicken tranquilized to the point of immobility with Acepromazine. Acepromazine was injected intravenously into superficial veins under each chicken's wing. Immobility was defined as no response by the chicken to a hand waved rapidly before its eyes. The dosage required to achieve this state for at least 30 min varied between .5 and 2.5 cm³ per bird. The other exposure period involved an untranquilized chicken.

Table 3: Frequency of different types of approaches made to both an active and a tranquilized chicken by Trustworthy Protecting Dogs (N = 12), Untrustworthy Protecting Dogs (N = 11) and Conducting Dogs (N = 10), in terms of row %.

State of chicken	Type of dog	Approach made to chicken (in row %)					Total No. of approaches
		Play	Invest.	Submiss.	Pred.	Domin.	
Active	TPD	<i>19</i>	<i>75</i>	0	0	6	16
	UPD	<i>51</i>	<i>40</i>	0	0	9	85
	CD	9	8	0	<i>83</i>	0	77
Tranquil.	TPD	14	<i>86</i>	0	0	0	21
	UPD	8	<i>83</i>	0	0	9	53
	CD	<i>14</i>	<i>28</i>	0	<i>54</i>	4	76

Italics indicate that row % is > 15.

Half the dogs, randomly selected, in each group (i.e., TPD, UPD, CD or wolves), were exposed to an untranquilized chicken first, while the other half were exposed to a tranquilized chicken first. Only one presentation was made per day. Sampling procedures and types of data collected were nearly identical to those outlined in the last experiment. Statistical analysis differed in that direct comparisons could be made between the behavioral interaction patterns of the TPD, UPD, CD, wolves and coyote with the data from the two test periods.

Results

Within each group, individual dogs displayed qualitatively and quantitatively similar motor patterns to the prey regardless of order of presentation. Because this intra-group behavioral homogeneity existed, the data for dogs within each group were combined.

Table 4: Frequency of different behaviors exhibited to an active chicken following an approach by Trustworthy Protecting Dogs (N = 12), Untrustworthy Protecting Dogs (N = 11) and Conducting Dogs (N = 10), in row %. The intermediate response of the chicken to the dog's approach is ignored.

Type of dog	Initial approach by dog	Subsequent behavior dog exhibited (in row %)					Total No. of initial dog approaches
		Play	Invest.	Pred.	Mouthing	Terminate interaction	
TPD	Play	50	0	0	0	50	2
	Invest.	17	17	0	0	67	12
	Predatory	0	0	0	0	0	0
UPD	Play	44	21	9	16	9	43
	Invest.	22	56	0	9	13	32
	Predatory	0	0	0	0	0	0
CD	Play	43	0	14	43	0	7
	Invest.	0	17	33	50	0	6
	Predatory	2	3	89	0	6	62

Italics indicate that row % is > 15 when the total number of initial approaches is > 2

The interaction of the 15-year-old wolf with the active chickens was composed of the following sequence:

eye — stalk — (chicken fled) — predatory-chase — grab-bite — crush-bite — eating behavior.

Some variation was seen in the individual predatory behavior of the wolves (SULLIVAN 1979). The 3-year-old wolf also killed and consumed the active chicken but it interspersed a motor pattern more commonly seen in play into its predatory sequence in the following fashion:

bow' — crush-bite — head-shake — play-bow — eating behavior.

The coyote's approach and subsequent motor patterns with the tranquilized chicken occurred as follows:

eye — stalk — grab-bite — carry chicken — crush-bite — eating behavior.

The sequence of motor patterns displayed by the coyote with the active chicken was the same as the sequence outlined above with the exception of carry chicken which was deleted. Although this observation is based on only one coyote, the active chicken appeared to elicit a much more tenacious predatory sequence than did the tranquilized chicken. Both wolves and the coyote killed and consumed the tranquilized as well as the active chickens.

Table 3 shows the various approaches made to active and tranquilized chickens by the three groups of livestock dogs. An observed change in dog behavior elicited by reducing chickens' activity was the increase in investigatory approaches in all dogs. This investigator's increase was at the expense of play approaches in UPD and predatory (eye/stalk) approaches in CD.

Tables 4 and 5 show the percentages of five different behavioral responses made by TPD, UPD and CD to chickens following their initial approaches. Only

those data concerning play, investigatory and predatory (eye/stalk) approaches are reported because submissive and dominance approaches were exhibited only rarely.

CDs displayed primarily play and investigatory motor patterns to the tranquilized chicken. This behavior was preceded by play, investigatory, and, most often, predatory approaches. Typically, the CD would eye and stalk the tranquilized chicken and then appear to be “waiting* for the chicken to move. After a few s, if the thicken failed even to twitch its head, the CD usually began to bark, play-bowed, and then playfully lunged at the chicken. As soon as the chicken moved, even slightly, the CD would drop into eye, and then the sequence of behaviors just described would usually recur. To an active chicken, however, the CDs responded by exhibiting a greater percentage of predatory behavior.

Table 5: Frequency of different behaviors exhibited to a tranquilized chicken following an approach by Trustworthy Protecting Dogs (N = 12), Untrustworthy Protecting Dogs (N = 11) a Conducting Dogs (N =10), in row %

Type of dog	Initial approach by dog	Subsequent behavior dog exhibited (in row %)					Total No. of initial dog approaches
		Play	Invest.	Pred.	Mouthing	Terminate interaction	
TPD	Play	67	33	0	0	0	3
	Invest.	6	94	0	0	0	18
	Predatory	0	0	0	0	0	0
UPD	Play	0	50	0	50	0	4
	Invest.	5	55	2	34	5	44
	Predatory	0	0	0	0	0	0
CD	Play	64	0	9	27	0	11
	Invest.	5	86	0	10	0	21
	Predatory	34	22	22	2	20	41

Italics indicate that row % is > 15.

Following their initial, almost always investigatory approaches to tranquilized chickens, the UPDs displayed primarily investigatory motor patterns. The number of play motor patterns that UPDs displayed toward tranquilized chickens was negligible, and this is in sharp contrast to their interactions with active chickens. UPDs were the only group of dogs that play-chased active chickens. Following these chases, the UPDs frequently engaged in playful interactions with active chickens. A typical example of one of these interactions was:

play approach — (chicken flees) — play-chase — mouthing chicken — pick up chicken — head-shake — release — play-bow.

Behaviors exhibited to tranquilized chickens commonly occurred in the context of investigatory behavior. A typical example of one of these interactions was:

investigatory approach — sniffing — licking — sniffing — licking — mouthing — sniffing — mouthing — carry chicken — head-shake — release.

Rarely, a motor pattern that can be used in both predatory and play contexts, such as fore-foot stab or head-shake, was observed interspersed with the play or investigatory behavior of UPDs. But on the few occasions that this did happen it was a single motor component expressed not as part of a functional predatory sequence but as an isolated occurrence in the context of a sequence of play or investigator) behaviors. Moreover, UPDs responded most frequently to the active chickens by turning away from them and terminating the interaction. What is most interesting, perhaps, is the low frequency with which TPDs approached either tranquilized or active chickens, relative to the total number of approaches displayed by the other two groups of dogs. Commonly, TPDs would respond to a chicken (regardless of its level of activity) by just wagging their tails or assuming investigatory postures. Patterns of interaction displayed by the TPD relative to the other two groups of dogs were, quite simply, more passive. They approached chickens less often and consequently interacted with them less often.

Discussion

Only occasionally, throughout this study, would an observer report seeing in either TPDs or UPDs even a single component of predatory behavior, and even then this component (such as a fore-foot stab) was expressed in the context of a behavioral sequence with social play behaviors predominating.

In contrast to both types of protecting dogs, conducting dogs were most often observed to relate to the chickens, as to the sheep in earlier studies, as predators to prey. Their predatory behavior was characterized by the integration of the motor components eye, stalk, and chase into a behavioral segment that makes it easy to truncate the full linear wolf sequence after chase, with a motor-trap or loop in its predatory program that tended to take the dog back through eye-stalk-chase rather than on to crush-bite, dissect and ingest. A “motor-trap” is a typically youthful mammalian behavioral phenomenon noted by Fentress (1983) that unexpectedly interrupts a stereotyped functional sequence. CDs tended to repeat and terminate their predatory program at the appetitive stage. In clear contrast, throughout this experiment with chickens, dogs, wolves and coyote, wild canid predatory behavior was characterized by the stereotypically linear sequence of a fully functional system (Fox 1978; Zimen 1981).

In both types of protecting dogs play-bites and play-chases were apparently

separable motor units of their behavior system that may be combined at any opportunity with other motor units to produce non-functional, non-systematic sequences of mixed social behaviors that strung together are commonly referred to as “play” behavior. Each motor pattern was more discrete in PDs than in CDs, less a component of any stereotypical sequence. As a result, PD behavior was characterized by non-goal-oriented sequences of mixed social canid behavior patterns.

The major differences among percentages of various approaches by all three types of dogs to sheep (Table 1) and to active chickens (Table 3) was the tendency of TPDs to exhibit a greater number of submissive approaches to sheep and, conversely, a greater number of investigatory approaches to active chickens.

The argument that PDs lack the predatory sequence, rather than possess a conditioned inhibition of the sequence, is strengthened not only by our failure to find a threshold effect but more importantly by the perpetual displays even in adult PDs of a juvenile behavioral repertory whose onsets during ontogeny precede the onset of the predatory sequence. Early Eurasian herdsman may have achieved an ontogenetic stage of development that preceded and precluded the onset of predatory behaviors, thus creating a type of protecting sheepdog that was not only non-predatory but youthfully capable (even when adult) of social bonding to other species (Coppinger & Smith 1983). The ontogenetic stage selected in conducting sheepdogs was not as retarded as that of the protecting dog. Conducting dogs retained at least a segment of the full ancestral predatory sequence and thus relate to sheep not as conspecifics but more as objects to eye-stalk-chase.

Conclusion

Two distinct sets of behaviors were displayed by CDs and PDs when first presented to sheep as juveniles, in spite of being raised together in the same environment. Partial predatory behavior (such as eye/stalk/chase) was characteristic of adult CDs, whereas adult PDs continued to show a high level of play, investigatory, and submissive behavior characteristic of young canids.

Within the protecting dog type were extremes of behavior that ranged from sheep protecting to sheep killing. In spite of this conflict of expectation, no predatory sequences and only minimal display of even single predatory motor patterns could be observed in the protecting type at either extreme. Investigation of this variation in PD responses to sheep reaction revealed no variation in kind of motor behavior that they expressed, nor any variation in degree of predatory behavior but, rather, a marked variation in the frequency of play behavior. The untrustworthy protecting dogs were more active and more likely than trustworthy dogs to play with sheep. Sheep responded differently to different approach

patterns by dogs. A pattern emerged between the type of approach the dog made, the type of response the sheep made, and the subsequent behavior of the dog. Play approaches by protecting dogs were more likely to cause sheep to flee. Regardless of initial approach pattern, if a sheep fled from a dog, the dog's subsequent behavior was more likely to be continuously playful.

In a final attempt to elicit a predatory sequence in protecting dogs we changed the livestock from sheep to chickens. The chickens still failed to elicit significant predatory behavior from either extreme (trustworthy or untrustworthy) of protecting dogs. The new stimulus altered only the frequency but not the quality of livestock dog behavior.

In several behavioral systems (play, investigatory, submissive, predatory) a concordance in frequency of display with developmental stage has been noted. Bemis (1984) argued that when one finds concordance within different organ systems, one need not assume that there was a selective force for each component, but rather that "correlated changes are believed by Alberch et al. 1979 to be a common component of heterochronic processes such as paedomorphosis." If the same argument could be used for the evolution of behavior, then a selective advantage for each behavior "organ" system would not be required but rather a concordance in the derived behavioral characteristics with an ancestral ontogenetic stage.

A point by point mutation hypothesis for these two types of sheepdog is difficult to imagine. One can imagine Eurasian shepherds selecting against predatory sequences, but why select for social play that in PDs is a fault (Darwin 1845; Coppinger et al. 1983 b)? One can also imagine British shepherds selecting for predatory routines, since these are what enable CDs to approach and direct the sheep (Vines 1981; McConnell & Bayliss 1985), but why select against social play that in herding dogs is not a fault?

In addition to the behavioral correspondences between PDs and CDs to different phases of youthful ancestral behavior, the morphological correspondence between PDs (that as adults retain infantile or embryonic characters such as floppy ears and domed skull) and CDs (that display a less rounded, more adult shaped skull and retain throughout life half-erected ears) (Coppinger & Coppinger 1982), helps make more interesting the possibility that the two types of livestock dogs are neotenic polymorphs unconsciously selected by differential retardation of ontogeny.

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