

Paedomorphosis affects agonistic visual signals of domestic dogs

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Abstract. Many of the structural modifications of modern breeds of domestic dog, *Canis familiaris*, can be explained by changes in the rate of development, during domestication from the wolf, *C. lupus*. These changes have been dominated by paedomorphosis, or underdevelopment, so that the adult passes through fewer growth stages and resembles a juvenile stage of its ancestor. In this paper the effects of these processes on the signalling ability of 10 breeds selected for their degree of physical dissimilarity to the wolf are examined. The number of ancestral dominant and submissive behaviour patterns used during signalling within single-breed groups ranged from two (Cavalier King Charles spaniel) to 15 (Siberian husky), and this correlated positively with the degree to which the breed physically resembles the wolf, as assessed by a panel of 14 dog behaviour counsellors. When the signals displayed by each breed were grouped according to the stage of wolf development in which they first appear, those breeds with the smallest repertoires were found to draw most of their signals from those appearing before 20 days of age in the wolf, suggesting that physical paedomorphism has been accompanied by behavioural paedomorphism.

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Paedomorphosis, the retention of juvenile morphology at maturity, is thought to be an important process in generating evolutionary novelties (Gould 1977). Much of the evidence for paedomorphosis comes from the fossil record (Morey 1992), making its interaction with behaviour difficult to assess. However, it must logically have an effect on visual and other modes of communication, if the development of the signalling structures is altered relative to other morphological features. The development of behaviour may also be affected more directly, via effects on the central nervous system. For example, Lorenz (1971) argued that the retention of inquisitive behaviour into adulthood in humans is a consequence of neoteny (i.e. a slower rate of development).

Heterochrony is defined as a change in the timing of rate of developmental events, relative to the same events in the ancestor (Sheldon 1993). Paedomorphosis results in a reduction in the rate of change in development, so that the descendant adults pass through fewer stages of growth and

resemble a juvenile stage of the ancestor (i.e. underdevelopment). Paedomorphosis can be subdivided into three further categories: neoteny (as defined above), post-displacement (later onset of development) and progenesis (earlier completion of development). Peramorphism is the opposite heterochronic process to paedomorphosis and results in a prolonged period of growth or development, relative to the ancestral condition. It can also be considered to comprise three categories: acceleration (a faster rate of development), pre-displacement (earlier onset of development) and hypermorphosis (later completion of development). These heterochronic processes can affect the whole developmental process (global effects), or be restricted to certain developmental events (local effects), and more than one process may be effective simultaneously (mosaic heterochrony) (Sheldon 1993).

The domestic dog, *Canis familiaris*, was domesticated from the wolf, *C. lupus* (Clutton-Brock 1995). Although it is now classified as a single species distinct from the wolf, the dog exhibits considerable morphological diversity, much of it thought to be the result of both global and local paedomorphosis. In the literature this is usually described as neoteny (e.g. Coppinger et al. 1987),

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but some aspects of variation between breeds, such as overall reduction in growth (see Figure 13 in Hedhammer 1982), are clearly the product of global progenesis (sensu Sheldon 1993) in addition to neoteny, since small breeds achieve adult weight earlier than large breeds, as well as growing more slowly. More complex heterochronic processes have been detected in the Alaskan malamute, in which the development of the skull is initially delayed compared with that of the wolf, so that neonates appear 'fetal' by comparison with wolf cubs, and then accelerates to produce a wolf-like head in the adult (Frank & Frank 1982). Early sexual maturity in the dog compared with the wolf (Fox 1978) could indicate either pre-displacement, or acceleration. However, the vast majority of breeds of dog are paedomorphic in body shape compared with the wolf, and therefore present an opportunity to examine the effects of paedomorphism on behaviour, and signalling in particular.

Visual communication between domestic dogs (reviewed by Bradshaw & Nott 1995) is conventionally described in terms of the signals performed by the wolf during dominance/submission interactions within the pack (Scott & Fuller 1965; Abrantes 1987). Inherent in this convention is the assumption that, during the 12 000 years since the dog began to be domesticated, the behavioural repertoires of the two species have not diverged. Whilst such an assumption may be valid for breeds of dogs that have retained a wolf-like appearance, in many modern breeds most or all of the ancestral structures used for signalling (e.g. the muzzle, the area around the eyes, the ears, the tail) have been substantially modified by selective breeding. Some of these changes have arisen by mutations in structural genes unrelated to heterochrony (e.g. the curled coat of breeds such as the poodle). Most, however, appear to have arisen from mutations in regulatory genes, causing retention of juvenile features into adulthood, including the threshold for aggression (Kretschmer & Fox 1975). Dogs showing such paedomorphism often exhibit a reduction in overall body size and retain a juvenile head:body ratio (Frank & Frank 1982; Price 1984).

In this paper, we set out to examine whether the variation in signalling repertoire between breeds is correlated with the degree of dissimilarity in overall appearance from the wolf. We also tested the hypothesis that the breeds with the most restricted

repertoires exhibit behavioural paedomorphism, that is, their repertoire is restricted to those patterns emerging earliest in the development of the wolf cub.

METHODS

We selected 10 single-breed groups of dogs that had lived together as social groups for at least 1 year (N =number in group; see Table I). Breeds studied were Cavalier King Charles spaniel ($N=6$), Norfolk terrier ($N=6$), Shetland sheepdog ($N=5$), French bulldog ($N=5$), cocker spaniel ($N_1=4$; $N_2=4$), large munsterlander ($N=4$), labrador retriever ($N=6$), German shepherd ($N=7$), golden retriever ($N=7$) and Siberian husky ($N_1=6$; $N_2=7$). These breeds show a range of ancestral signalling structures from the relatively wolf-like Siberian husky to the heavily modified Cavalier King Charles spaniel (Bradshaw & Nott 1995; Clutton-Brock 1995).

We observed each group in its familiar home environment and all sessions were videotaped for later observation in the laboratory. We observed each breed for a minimum of 3 h and recorded 15 different agonistic patterns of behaviour (Tables I and II), representing the most important signals shown by wolves during escalating displays of dominance and submission. Ear signals could not be reliably recorded from videotape for breeds with heavily modified ear structures, and so were omitted for all breeds. Inter-observer reliability was tested for three breeds, Siberian huskies, large munsterlanders and Cavalier King Charles spaniels which represent the extremes of physical similarity to the wolf, and one intermediate breed. The two observers (D.G. and S.M.W.) agreed exactly on the number of signals performed by each breed.

We began each study session by observing the animals interacting in the absence of external stimulation. We then introduced additional stimuli one at a time; these consisted of the owner, an unfamiliar person, food, toys, shelter, and familiar and unfamiliar dogs. This was intended to induce competition between group members over a variety of resources, and provide many opportunities for agonistic signalling in the relatively small amount of time available for observing each group. It was not possible to use all stimuli on every study visit, and an unfamiliar dog

Table I. Breed group information and observation times

| Breed | Sex and age (years) | Housing | No of sessions and observation time |
|-------|-----------------------------|------------|-------------------------------------|
| CK | 6f (1.5–10) | House dogs | 5# 1 h |
| NT | 3f (1–3) 3m (1) | House dogs | 1# 3 h |
| SS | 3f (3–13) 2m (8 and 9) | House dogs | 5# 1 h |
| FB | 4f (1.5–5.5) | Kennelled | 5# 1 h |
| CS | N_1 3f (1.5–9) 1m (8) | House dogs | 3# 1 h |
| | N_2 3f (7–12) 1m (7) | House dogs | 3# 1 h |
| LM | 3f 1m (age unknown—rescued) | House dogs | 5# 1 h |
| LR | 4f (1–4) 2m (1.5–4) | Kennelled | 3# 1 h |
| GS | 6f (1–13) 1m (8) | House dogs | 1# 3 h |
| GR | 4f (1.5–7) 2m (5 & 7) | House dogs | 3# 1 h |
| SH | N_1 1f (3) 5m (1–7.5) | Kennelled | 5# 1 h |
| | N_2 6f 1m (age unknown) | House dogs | 5# 1 h |

CK: Cavalier King Charles; NT: Norfolk terrier; SS: Shetland sheepdog; FB: French bulldog; CS: cocker spaniel; ML: munsterlander; LR: labrador retriever; GS: German shepherd; GR: golden retriever; SH: Siberian husky. f: female; m: male. N_1 : Group 1; N_2 : group 2.

Table II. Definition of behaviour patterns based on agonistic signalling observed in wolves

| Behaviour | Definition |
|-------------------|--|
| Threats | |
| Growl | Aggressor produces an audible low-pitched rumbling noise (Fox 1970) |
| Displace | Aggressor causes opponent to move away from a resource or goal (Schenkel 1967) |
| Stand over | Aggressor stands next to an opponent and holds its head over opponent's body, or more extremely places its forepaws on the opponent and raises its own head and chest over the body of the opponent (Fox 1969) |
| Inhibited bite | Aggressor places its jaws around part of the opponent's body, without fully closing them (Fox 1970) |
| Stand erect | Aggressor raises itself to its full height, with arched back, raised head and sometimes raised hackles (Fox 1969) |
| Body wrestle | Opponents stand on their back paws, while wrestling with forepaws, often while gaping (Fox 1969) |
| Aggressive gape | Aggressor half opens jaws and vertically raises the lips to expose the teeth (Fox 1970) |
| Bare teeth | Aggressor vertically raises the lips to expose the teeth (Fox 1970) |
| Stare | Aggressor looks directly at opponent maintaining eye contact (Fox 1970) |
| Submission | |
| Muzzle lick | Submissive animal licks at muzzle of opponent, sometimes without contact (Fox 1970) |
| Look away | Submissive animal averts its eyes from aggressor and turns its head away in a slow, exaggerated manner (Fox 1970) |
| Crouch | Dog lowers its head and body, often tucking the tail between the legs (Fox 1969) |
| Submissive grin | Dog draws lips back horizontally to reveal teeth with jaws closed (Fox 1970) |
| Passive submit | Dog lies on its back exposing ano-genital region (Fox 1969) |
| Active submit | Submissive animal approaches aggressor, in a crouched position, with the tail tucked between the hind legs and may attempt to lick the side of the aggressor's muzzle (Fox 1969) |

was not used with particular breed groups if their owner felt it would be unsafe to do so.

We included a pattern in the repertoire of a breed if it occurred once or more during the

observation period, during intra-group social interactions only (excluding interactions between group members and introduced dogs, which were usually not of the same breed). We do not claim

Table III. Behaviour patterns observed in normal social interactions within permanent groups of dogs

| Behaviour | CK* | NT | SS | FB | CS | ML | LR | GS | GR | SH | WO |
|-------------------|-----|----|----|----|----|----|----|----|----|----|-------|
| Threats | | | | | | | | | | | |
| Growl | + | + | + | + | + | + | + | + | + | + | <20 |
| Displace | + | + | + | + | + | + | + | + | + | + | <20 |
| Stand over | | | | | | + | + | + | + | + | 20–30 |
| Inhibited bite | | | | | | + | + | + | + | + | 20–30 |
| Stand erect | | + | | + | + | + | + | + | + | + | >30 |
| Body wrestle | | | | | + | + | | + | + | + | >30 |
| Aggressive gape | | | | | | | + | + | + | + | >30 |
| Bare teeth | | | + | | | | | + | + | + | >30 |
| Stare | | | | | | | | | | + | >30 |
| Submission | | | | | | | | | | | |
| Muzzle lick | | | + | | | | + | + | + | + | <20 |
| Look away | | | | + | + | | | + | + | + | 20–30 |
| Crouch | | | | | | + | + | + | | + | 20–30 |
| Submissive grin | | | | | | | | | + | + | 20–30 |
| Passive submit | | | | | | | + | | + | + | >30 |
| Active submit | | | | | | | | | | + | >30 |

See Table I for breed names. WO: Wolf; figures indicate first appearance of pattern in wolf development, in days (Fox 1969, 1970).

that these behaviour patterns represent an entire agonistic ethogram for each breed, as we were not attempting to induce overt aggression between dogs, owing to the obvious welfare risks, and we accept that infrequently used signals may not have been detected by this method. However, we believe that these signals represent the main agonistic signals commonly used between members of established single breed groups during intra-group interactions, and that any underrepresentation of signals used would be consistent between breeds.

The degree to which each breed's physical appearance differed from that of the wolf was assessed by 14 members of the Association of Pet Behaviour Counsellors (P.O. Box 46, Worcester, WR8 9YS, U.K.). Each was sent a questionnaire which asked them to score on a scale of 1–5 the extent to which they felt each of the breeds resembled an adult wolf, for the following eight signalling structures: length of muzzle, eyes, shape of ears, ability to move ears, coat, tail, overall proportions of head and body, and ability to alter the height of the back from the ground. The recipients were unaware at the time of the purpose of the questionnaires. The arithmetic mean of these scores was used as an indicator of each breed's overall similarity to the wolf.

RESULTS

The videotaped observations showed that each breed performed a different range of ancestral dominant and submissive behaviour patterns during intra-group signalling (Table III), ranging from two (Cavalier King Charles spaniel) to 15 (Siberian husky). This diversity in behavioural repertoire correlated positively (Spearman $r_s = 0.839$, $N = 10$, $P < 0.005$) with the degree to which each breed physically resembles the wolf (Fig. 1). In other words, dogs that had been assessed as appearing least wolf-like in the morphology of signalling structures also exhibited the fewest wolf-like patterns of agonistic behaviour.

Since the 15 agonistic behaviour patterns develop progressively during the first 7 weeks of a wolf's life (Table III), we were also able to test whether the signalling repertoire was affected by paedomorphism. If this hypothesis were correct we should expect that most of the signals performed by breeds possessing few dominance/submission signals would be those signals that develop earliest in the wolf. The breeds were divided into three groups according to the total number of signals performed, and the signals classified by the time of their first appearance during the development of the wolf (Table IV).

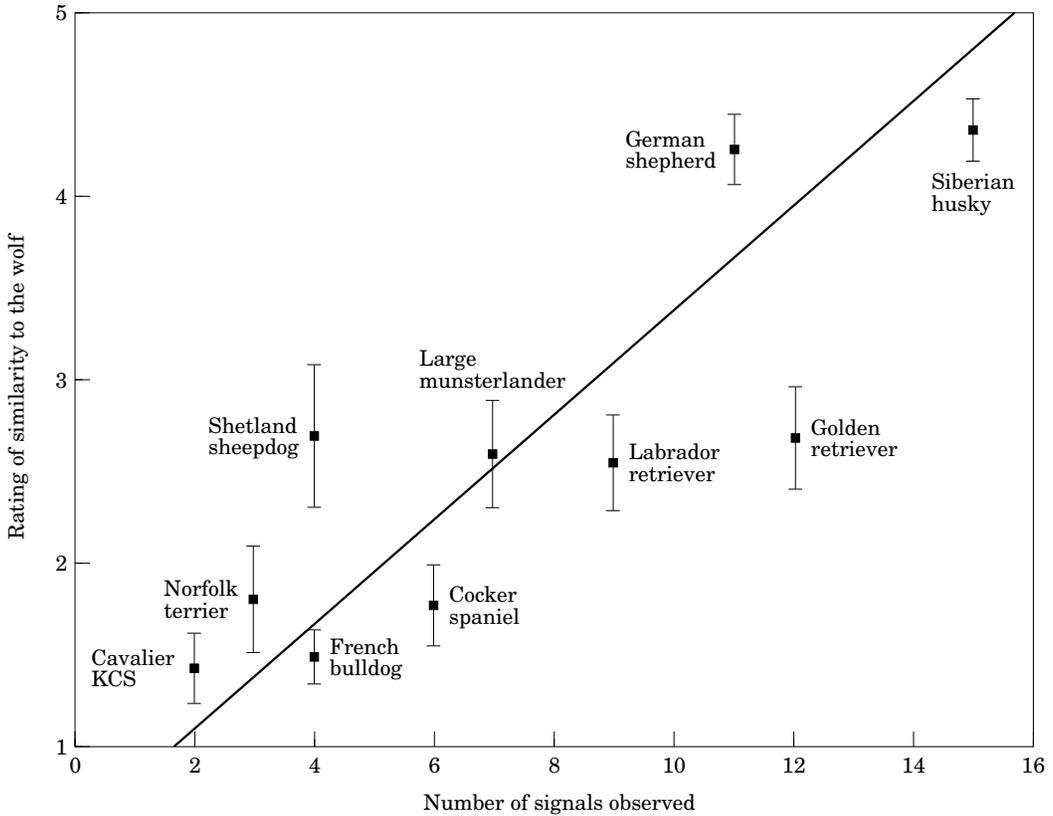


Figure 1. Relationship between the number of signals performed by each breed with its degree of similarity in appearance to the wolf (average of eight characteristics). Bars indicate standard deviations.

Table IV. Average number of wolf-type signals in the 10 breeds, divided into three groups according to the total number of signals observed classified by the developmental stage at which they first appear in the wolf

| Breed group | Signals (Range) | Wolf (0–19 days) | Wolf (20–30 days) | Wolf (>30 days) |
|----------------|-----------------|------------------|-------------------|-----------------|
| CK, NT, SS, FB | 2–4 | 2.3 | 0.3 | 0.8 |
| CS, ML, LR | 6–9 | 2.3 | 2.7 | 2.3 |
| GS, GR, SH | 11–15 | 3 | 4.3 | 5.3 |

See Table I for breed names.

The data in Table IV were tested for association by ANOVA using a two-factor model (wolf stage, breed group) with breed nested within group. This yielded an *F*-ratio for the interaction between wolf stage and breed group of $F_{4,14}=13.5$ ($P=0.0001$). The most restricted repertoires (first group) are drawn largely from patterns occurring early in the development of the wolf.

DISCUSSION

We have shown that the further the domestic dog has diverged from the appearance of the wolf, the more elements of lupine ‘body-language’ have been lost. If this process had affected the development of the brain and nervous system as well as the skeleton, we should also expect to see only

infantile wolf behaviour patterns in the most physically paedomorphic dogs. By classifying the behaviour patterns produced by each breed according to the age at which they first appear in the wolf, we have shown that this is likely to be the case.

Although we have demonstrated that breeds vary in the number of wolf-type signals they give, we have not considered whether these signals are received by the other members of the group (although we have no reason to suppose that they are not), or whether the information contained in the signals has diverged from the ancestral state. However, the division into Threats and Submissive signals (Table III), based on the wolf (Fox 1969, 1970), is upheld at least in the Siberian huskies. Both groups studied were worked in sled teams and the owners deliberately retained pack structure. In both groups the number of wolf-type threats performed within each pair-wise relationship correlated negatively with the number of submissive behaviour patterns displayed, as expected (Wickens 1993).

Three of the four gundog breeds (cocker spaniels, labrador and golden retrievers) retained more wolf-type behaviour patterns than their appearance would suggest, as seen by their position below the line of best fit in Fig. 1. The fourth gundog breed, the large munsterlander, a pointer, retains only slightly fewer behaviour patterns than its physical appearance would suggest. It would appear that the purpose for which these breeds were developed required the maintenance of a fuller range of ancestral behaviour patterns than the two breeds derived from shepherding stock (German shepherd and Shetland sheepdog). The physical appearance of these two breeds is more wolf-like than their behavioural scores would predict, suggesting that once a behaviour has been lost from the repertoire it cannot be reconstructed merely by altering the physical appearance of the breed. The German shepherd, which was developed from shepherding stock with the deliberate intention of producing a physically wolf-like animal (Willis 1991), displayed fewer wolf-type signals than did the Siberian husky and the golden retriever. The rate of signalling was also much lower than observed in the golden retrievers, little play took place and we gained the impression that signals given and received were due to actual conflicts over resources between the individuals concerned. The owners maintained close super-

vision of the animals at all times, in order to prevent escalation of aggression resulting in injury.

Circumstantial evidence suggests that the functions of the signals may have altered slightly in the more highly domesticated breeds. For example, the golden retrievers, which displayed 12 of the wolf-type signals, did so at a much higher frequency than the huskies and German shepherds. The signals were used extensively in play, with little escalated aggression shown, such that the owners were happy to allow the animals to indulge in highly boisterous play without fear of injury. The apparently playful nature of the signalling in this highly 'immature' breed (Bradshaw et al. 1996) would suggest that the cost of signalling has been greatly reduced, probably a consequence of domestication, since real competition for resources is negligible because of provisioning by humans. The persistence of the original function of the signals is clear when competing over a highly valued resource, but the high frequency of playful signalling supports the idea that domestication has encouraged the maintenance of juvenile social play behaviour in the adult animal.

In all six of the breeds with seven or fewer signals, very few (one or none) of the signals were of the type associated with submission in the wolf. This further supports the idea that the costs of escalated aggression have been reduced in the dog, because of human provisioning. In wolves the function of agonistic signals is to regulate the escalation of aggression during social interactions. The signals appear to provide interacting individuals with information about their opponent's competitive ability (Fox 1971). Without such regulation, frequent competitive interactions would be costly because individuals would repeatedly sustain wounds adversely affecting their ability to compete for access to resources such as food, shelter and mates. In domestic dogs the exhibition of escalated aggression to conspecifics is likely to be less costly than for the wolf because of human intervention during and after conflicts. Thus the cost of failing to display submissive behaviour is reduced, permitting its elimination from the repertoire.

As many of the animals in the study groups were related to some extent, and communication within the groups may be affected by the conventions of those groups, it must be stated that the

agonistic signals described here may not be comprehensive for all individuals of the breeds. It is also possible that more signal types would be used during unsupervised communication with strange dogs, or with dogs of other breeds. The most important behavioural signals for regulating aggression in mixed breed groups of dogs are those associated with posture, particularly the ability to alter the height of the body from the ground (Netto et al. 1992). It is interesting that in our study, eight of the 10 breeds exhibited the 'stand erect' posture, which does not appear until about 40 days in the development of the wolf, and this posture occurs even in two of the four most paedomorphic breeds (Norfolk terrier and French bulldog). It is possible that this ability has been retained because it is important in communication between dogs of different breeds, although olfactory communication is also important in such encounters (Bradshaw & Lea 1993).

The behaviour of the domestic dog may illustrate what happens to visual signals when natural selection is relaxed. Studying the behaviour of domestic animals may, therefore, provide useful information about the evolution of signalling and communication. The consequences for the dogs of losing so many apparently important visual signals can only be guessed at. The process is virtually over now for the established breeds which are more or less fixed by their breed standards; however, even these standards change gradually over time and new breeds continue to be developed.

The function of these signals within the wolf pack is largely to prevent the escalation of aggression, and since most breeds of dog have higher thresholds for aggression than wolves they may not need such a complicated body language. It is also possible that many dogs rely on olfactory signals that have been less modified by domestication, and/or subtle visual signals that have arisen de novo but have escaped the notice of biologists intent upon measuring wolf-type signals.

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