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Q&A

How did you become involved in doing research?
Undergraduate research is encouraged and well publicized at KU, so I approached several labs. I worked in the lab of Deborah Smith before working with Raymond Pierotti.

How is the research process different from what you expected?
It is much more reading of current literature than I had expected (or hoped for). I did not know I would like it so much, or want so strongly to make an impact, however small, on my field.

What is your favorite part of doing research?
Finding results in the data. The statistical tests were interesting, and calculating the significance of everything I worked toward was humbling, yet rewarding.

Effects of paedomorphosis on signaling behaviors in dyadic encounters of the domestic dog

Jennifer Aucott

ABSTRACT
Domestic dogs, *Canis lupus* (variety *familiaris*), show extremes of morphological variation in comparison to their ancestor, the wolf (*Canis lupus*), with some breeds being much smaller than a typical wolf (males 40-60 kg, females 30-45kg), while other breeds are much larger. A major trend observed to be a result of the process of domestication is paedomorphosis, or retention of juvenile traits into adulthood. Dogs express paedomorphic traits to different degrees, ranging from phenotypes that resemble wolves to extreme forms such as toy dogs, with short muzzles and legs. These traits can be both morphological to behavioral in nature. Such traits must interact because morphology is used to express behavior. One key example of this is the use of both ear and tail orientation to signal status in interactions among dogs. By observing dyadic encounters, I measured the extent of paedomorphic reduction of the ability to use signaling behaviors, specifically those involving the ears and tails. I did not find a correlation between overall paedomorphosis and frequency of signaling, but did find significant interactions between signal frequency and the degree of dissimilarity of the tail of individual breeds from a wolf tail. Despite this interaction, I found that signaling was consistent across breed types and sizes. This indicates that signaling is highly conserved and evolutionarily important, even across

a large range of phenotypes. When tail signaling is reduced, it is often associated with a highly variant tail, especially those artificially shortened by human action.

INTRODUCTION

It has been established that the ancestors of all domestic dogs are wolves, and this domestication occurred several times across the world (Morey 1995). Along each of these separate lineages, the domestication process has yielded a variety of animals whose mature morphology shares traits with the juveniles of its ancestral form.

Termed paedomorphosis (Gould 1976), this phenomenon is not unique to the domestic dog; it appears in virtually all domesticated animals. A major process in domestication, it allows a lowered reproductive age and heightened threshold of aggression (Kretchner 1975). One can easily speculate why humans may select for these traits. However, the paedomorphosis also occurs naturally in numerous wild species, such as the axolotl (compared to its ancestral salamander form) and modern humans (derived from australopithecines).

In the dog, *Canis lupus* (variety *familiaris*), physical paedomorphic traits often include a large, rounded skull, a shortened muzzle, folded ears, a curled or shortened tail, and small size (but see lupine breeds below). Behavioral traits include a propensity toward play, heightened threshold of aggression, and increased barking in comparison to the dogs' wild ancestor, *Canis lupus* (Morey 1993). These qualities have been cultivated under the protection of humans. In this context, survival pressures were not as strong as in the wild. Deviation from the ancestral wolf did not reduce the dog's chance of survival and reproduction, regardless of its impact on overall health and fitness.

Dog breeds exhibit paedomorphosis to various degrees. So-called lupine breeds, such as huskies, malamutes, and samoyeds, retain more characteristics of an adult wolf, and less of the appearance of a juvenile wolf; this contrasts to many toy breeds (Pekinese, Cavalier King Charles spaniel) whose unnaturally short muzzles, folded ears, and rounded skulls serve as evidence of extreme paedomorphosis.

One impact of such a drastic change in morphology is a reduction in tendency to communicate (via visual body signals) with other dogs. A major role of canid communication is the maintenance of a relatively peaceful and stable social setting through establishment of dominant and subordinate roles to reduce potential physical conflicts among other dogs.

If we look at the wolf's behaviors, they consist of postures and movements. Table 1 shows several commonly seen behaviors, taken from Goodwin (1997). These are more extreme signals that convey dominance or submission; less exaggerated signals are also used.

The interaction between dominance and submission is critical to have smooth functioning within group relationships. As illustrated by

TABLE 1.

Dominant Behaviors	Submissive Behaviors
Stiff, erect stance	Crouch
Tail raised	Tail tucked down between legs
Ears forward	Ears flat
Direct stare	Licking or "grinning" at the face of another animal
Muzzle grab	Arched back
Sniffs recipient's groin	Tail wag
Foreleg across subordinate's shoulders	Rolls onto back

Mech (1999), these demonstrations can be used in situations of food-begging, conflict avoidance, promotion of peaceful relationships, and food distribution. For example, older offspring will frequently eat before younger siblings; however, wolf parents may preferentially feed growing pups, rather than offspring of an older litter, when food is scarce (Mech 1999).

Through the process of domestication, human intervention has both added artificial selective pressures and relaxed natural selective pressures (Price 1984). This change can be manifested in signaling behavior. As humans regularly provide ample food and intervene in conflict situations, both the cost of aggression and the need for signaling have been relaxed. Therefore, signaling can lessen in intensity and frequency without causing harmful results, and can even be used in inappropriate contexts. Dogs may roll onto their backs before their dominant human not as a submissive signal, but rather to incite attention (Frank and Frank 1982); however, it can be argued that this attention-begging is an offshoot of the food-begging explained by Mech (1999).

Several researchers have investigated the relationship between signaling behavior and paedomorphosis. Goodwin et al. (1997) showed an inverse relationship between the level of paedomorphosis of a given breed (using the following traits: muzzle length; ear, eye, coat, and tail type; flexibility of back and ears; and body proportions) and its retention of wolf visual signals. Additionally, she showed that those breeds (or individuals) exhibiting fewer behaviors tended to perform behaviors that appeared earlier in wolf development, i.e. puppy or juvenile-type behaviors.

Goodwin et al. (1997) observed almost no submissive behaviors in the breeds whose communicative signals were reduced. She argues that because humans intervene so frequently in an aggressive situation, the cost of aggression is lowered, and therefore the need for submissive signaling is reduced. Similar reduction is also seen in wolf puppies, which are largely protected by their youth. Adult dogs rarely attack puppies, and this reduction of aggression may apply—to some extent—to small or paedomorphic dogs. An apparent contradiction can be found in the study of Bradshaw and Lea (1992), which observed that some "subordinate" behaviors (namely, a resistance to being sniffed by others) occurred more frequently in dogs than in wolves. This typically submissive action was frequently seen in both dogs in a dyadic encounter.

Physical limitations in these breeds are probably largely responsible for decreased signaling. For example, a Maltese may not be able to convey a submissive message by flattening its already drooping (also obscured by long hair) ears. Some breeds, although wolf-like in basic behavior, have lost some behavioral variants, e.g. Border Collies are incapable of howling and also have ears that tend to flop over in their natural carriage. Behavioral reduction can also occur without physical disability. Though a dog may be capable of assuming a submissive posture, the tendency to display this behavior may be decreased in paedomorphic dogs, because they already appear to be in a crouching position with lowered ears.

Some dogs also must cope with non-heritable modifications. The common practices of tail and ear docking may severely interfere with these signaling capabilities. Tail docking removes the majority of the tail, leaving a stub that may or may not be able to visibly convey social signals. Ear cropping is the removal of large portions of the pinnae. The resulting ears stand stiffly up or flop over near the top as in boxers and Boston terriers. These procedures are common in pit bulls, boxers, Doberman pinschers, and great Danes. Tail docking is also seen in some breeds of sporting dogs.

Unlike Goodwin et al. (1997), Bradshaw and Lea (1992) reported largely conserved behaviors across breeds. Though not examining individual signaling behaviors, but instead concentrating on regular action patterns, the authors described largely uniform behavior sequences. These include sniffing of the oral or anogenital regions. Bradshaw and Lea (1992) also noted humorously that the dog's size only slightly affected their tendency to attempt to end the interaction.

Also, in seeming contradiction to Goodwin et al. (1997)'s findings, Kerswell et al. (2009) found no significant difference in signaling related to paedomorphosis at this age. Authors observed intra-litter signaling of 5-week-old pups in a highly precise study of paedomorphosis. This observation could be due to the stage of development or the emphasis on intra-group observation. As the study notes, pups may not need to send strong, frequent signals with their littermates, with whom they have fairly well established social structures.

For this reason, it is necessary to test interactions between dogs that are not only mature, but which have no previous history, so the need for dominant or submissive postures would presumably be greatest. Dyadic encounters take on much different natures in dogs than in wolves. Where encounters between

wolf packs are sparse and often violent, dogs rarely display aggression when meeting others (Bradshaw and Lea 1992). Furthermore, a public setting (such as a dog park, where the study was done) will likely weed out dogs that have previously shown aggressive or fearful reactions to unknown dogs.

Researchers such as Goodwin et al. (1997) have drawn connections between degrees of paedomorphosis and displays of wolf-like behaviors, but specific traits have not been thoroughly researched. The goal of this experiment is to look more closely at two distinct signaling behaviors—the orientation of the tail and the ears during a dyadic encounter—and determine if the frequency of occurrence is related to 1) the dog's overall degree of paedomorphosis, or 2) the tail's and ears' degree of dissimilarity to those of a wolf. It would be expected that if paedomorphosis reduces mature ancestral behaviors, then the more the dog differs from its ancestral form, the less it should signal.

METHODS

Dyadic dog interactions were filmed at Shawnee Mission Park and Lawrence, Kansas Mutt Run, both of which are off-leash dog parks. Video recordings were taken of dyadic encounters between dogs with no known previous encounters. Data was taken from the videos as described in the following manner. 1) Tail change was measured by the difference between the initial and final angles (using vertically down as an initial point of reference). Measurement used only the angle of the base of the tail in an effort to detect motion in breeds that have curled or short tails. A lack of signal in any tail was marked as either "no change" (indicating visible lack of change) or "no data" (indicating the observer could not see the tail well enough to measure a change). 2) Ear change was taken as the movement forward or back (or no change). Again, the base of the ear was used in measurement so as to detect a similar pattern of movement in drop, erect, and cropped ears. Individual breeds were identified using breed standards from *The Complete Dog Book* (AKC). Mixed breeds were noted, and possible breed contributions were estimated. If the dog wagged its tail for most of the encounter, it was marked as wagging. If the dog had any following interaction with the other dog (such as play, aggressive, submissive or dominant behaviors), it was described.

Ear type was marked as drop, erect, or cropped. Cropped was separated from erect based on breed standards.

Tail types, as adopted from *The Complete Dog Book*, include:

- Bobtail: very short, either docked or natural
- Feathered: long, carried down, with fringe
- Flag: long, carried high, with fringe
- Otter: thick, tapering tail, carried down
- Ring: forms at least a half-circle, carried high
- Saber: forms a semicircle
- Whip: carried straight, skinny

Breed data were later lumped into broader categories by type of breed, e.g. sport, working, herding, and approximate weight: small (< 30lb), medium (30-60lb) and large (>60lb). These followed AKC's *The Complete Dog Book* guidelines, and in data analysis, the three most common groups were used.

Degree of paedomorphosis was also noted. Each breed received a score based on presence of the following: short muzzle, flop ears, big head (relative to overall body size), short or curly coat, and small size. Scores 0-1 had a low degree of paedomorphosis; scores 2-3 had medium; and scores 4-5 were marked as high.

Chi-squared tests were applied to the results from observing dyadic interactions, and significance was determined using an alpha-value of 0.05.

RESULTS

It appears that overall physical paedomorphosis did not impact the behavioral frequencies (Tables 2 and 3, $p>0.05$). Additionally, neither size nor breed type impacted signaling frequency (Tables 6-9, $p>0.05$).

There was a significant difference in signaling frequencies according to type of tail (Table 4, $p<0.001$). Those that were most likely to signal had either whip or feathered tails. Dogs with bobtails and ring tails were not observed to unambiguously signal with them, however, it is possible that the degree of movement is discernible to dogs but not to the observer. In contrast, ring tails are normally carried high so it would take a major effort to lower them on the part of the dog. Thus, it seems that these tails have diminished signaling capabilities. In contrast, tails docked halfway (marked as "half-whip" tails) appeared to signal as successfully as full tails (Table 4), suggesting that this type of docking has less behavioral impact on the dog.

Interestingly, there were no obvious differences in signaling among phenotypes using the ears (Table 5), implying that whichever mechanisms might be involved in reduction of tail signaling has not affected ear signals. Overall, ear signaling was much more common than tail signaling (88.24% and 61.76% of all dogs, respectively: see Table 10). Perhaps a clear ear signal is sufficient to convey a dominant or submissive role, allowing tail signaling to decrease in frequency in dogs.

As seen in Table 10, ear and tail movements were found to correlate significantly ($p<0.001$). There was some correlation of dominant signals, but the relationship was not nearly as strong as with both submissive signals. When the tail lowers, ears are likely to lie back as well. The majority of dogs that did not signal with their ears held their tails up. Likewise, most of those that signaled with ears forward did not change their tail orientation. It was rare that a dog would send crossed signals (ears forward and tail down, or ears back and tail up), implying that these signals serve an important role in social interaction and should not be confused. The vast majority of dogs gave some sort of signal (144 out of 154).

Tables 6 and 7 show the frequency of dominant and submissive signals by dog size. For the sake of clear role identification, the "absence of signal" category was removed from this table. Each size category followed the findings of Table 8; i.e. that ears back often paired with tail down, and dominant signals were likely to correlate, though with a weaker association. Small and medium dogs were most often found to show submissive signals, while large dogs were more likely to take a dominant role, shown in Table 11.

Tables 8 and 9 show tail and ear signaling by breed type; divided into working, herding and sporting groups. There were no significant differences among these groups, which supports the idea that these are universal signals among dogs.

DISCUSSION

Overall paedomorphosis

I originally hypothesized that the impact of physical paedomorphosis would positively correlate with the degree of behavioral modification, which was assumed to manifest as a decrease in signaling frequency of either ear or tail in a dyadic encounter. This experiment did not find any correlation between degree of overall paedomorphosis and signaling frequency. In contrast to the findings of Goodwin et al. (1997), overall physical paedomorphosis may not be an accurate predictor for behavioral paedomorphosis.

This topic requires further research. The nature of the study—observation at dog parks—generated a sample consisting predominantly of medium to large dogs, and very few of toy or companion groups. These smaller dogs are the clearest representatives of high paedomorphosis, thus their absence from the sample could prevent a robust conclusion on the matter. Another notable factor is that huskies made up a large portion of the low-paedomorphosis group, and this breed had ring tails, which consistently could not signal in a reliable fashion. In fact, some of the most lupine dogs (samoyeds, huskies, and malamutes) may have experienced artificial selection for ring tails that would not impede them when pulling sleds, but—coincidentally—would impede their communication. Lastly, the specific behaviors of ear and tail signaling could be conserved across dogs, and thus remain unaltered by behavioral reduction. If this were to be the case, it would indicate that these two signals are very important in dyadic encounters between unfamiliar dogs.

This result led me to consider two more hypotheses, each of which investigates a different measurement in place of overall physical paedomorphosis.

Dissimilarity of signaling feature

The first hypothesis is that dissimilarity of the signaling feature in itself may have a larger impact on its signal frequency. This hypothesis was investigated by separating dogs by tail type, which yielded a significant result. Those phenotypes with highly deviant tails (rings and bobtails) were found to signal much less frequently than those that had more wolf-like tails, i.e., tails that were held naturally lower than 90 degrees. Dogs with bobtails were often docked. Bobtails used in analysis were visible, so a lack of signal could indicate either a lack of behavior or, more likely, an inability to express the behavior. Either way, dogs with bobbed tails were not observed to display signals of dominance or submission.

The human practice of docking tails could present a danger in dyadic encounters, where the animals show no clear patterns of dominance and submission, because clear, unambiguous signaling allows two dogs to communicate their relationship without displays of violence. If communication is inhibited, likelihood of aggression, violence, and possible injury to one or both dogs increases. Thus, tail docking constitutes a potentially harmful alteration not only to morphology, but behavior as well. No conflict was observed in this study, which is likely in part a result of the pool of dogs that owners would deem safe for the public dog park. More research must be done on correlation between docking and violent encounters. Dogs were also analyzed by ear type. Drop ears are a paedomorphic trait, and thus might be used to signal less frequently. This was not observed to be the case, however, as drop, erect, and cropped ears were found to signal with similar high frequencies.

Size and breed type as variables

The second hypothesis tested was that breed type is a better indicator of behavioral paedomorphosis than physical appearance. For example, though sporting dogs appear highly paedomorphic, strong signaling capabilities may be crucial to human-dog communication, and may have been preserved.

Neither breed type nor dog size affected signaling frequency, however, which is notable in itself. Across a wide variety of phenotypes, including drastic changes in morphology, these signaling behaviors are relatively constant. Size of the dogs involved did, however, affect the frequency of assuming the dominant or submissive role.

Signal pairing

Data showed a strong correlation between use of ears and tails to indicate a submissive state, whereas the dominant signals showed a weaker correlation that might be a result of altered tail and ear structures. This strong concurrence of submissive signals indicates that clear submission is evolutionarily important because it reduces the likelihood of an aggressive interaction.

A dominant signal from either ears or tail was most frequently paired with a lack of signal in the other variable. Dogs taking a dominant role may be reluctant to broadcast multiple strong signals depending on the other dog's reception. It must be noted that dogs do not enter a dyadic encounter in the same manner each time; each signal should be seen as a reaction to the other dog and its specific behaviors. For example, it is likely that when meeting an extremely submissive or non-threatening dog (e.g. a puppy), strong dominant signals are unnecessary. There is also the possibility that unnoted dominance behaviors were taking place that served as stronger signals to the recipient in place of tail or ear signaling.

Given Goodwin's findings correlating paedomorphosis and behavioral reduction, I anticipated a clear link between paedomorphosis and signaling behavior of the tail and ears in dyadic encounters. This was not the case. Overall paedomorphosis has no significant relationship with these two signals (although the poor representation of toy and companion dogs calls for a more inclusive sample). Because the signals are also unaffected by breed function and size, I conclude that they are vital enough in dog communication to be conserved traits. Morphology of the tail serves as a better indicator of its signaling frequency; dogs with ring or bobbed tails appeared to have difficulty using them in interactions, likely due to physical disability. Dog owners should take these findings into consideration, especially when considering tail and ear docking. These signaling mechanisms are vital indicators of intent across breeds.

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TABLE 2. Tail signaling by degree of paedomorphosis

	Degree of Paedomorphosis			
	Low	Medium	High	**Total**
Tail Signal	12	63	15	**89**
Tail No Signal	14	32	13	**59**
Total	**26**	**94**	**28**	**148**

TABLE 3. Ear signaling by degree of paedomorphosis

	Degree of Paedomorphosis			
	Low	Medium	High	**Total**
Ear Signal	19	80	21	**120**
Ear No Signal	4	12	6	**22**
Total	**23**	**92**	**27**	**142**

TABLE 4. Tail Signaling by Tail Type

	Tail Type								
Tail change	Bobtail	Saber	Otter	Flag	Ring	Half-whip	Whip	Feather	**Total**
No Signal	14	8	7	7	15	6	0	3	**60**
Signal	4	20	17	8	9	10	4	20	**92**
Total	**18**	**28**	**24**	15	24	16	4	23	**152**

TABLE 5. Signaling by Ear Type

Ear Type	Signal	No Signal	Total
Drop	88	15	**103**
Erect	36	6	**42**
Total	**124**	**21**	**145**

TABLE 6. Tail signaling by size

	Tail Signal	No Tail Signal	Total
Small	20	12	**32**
Medium	51	27	**78**
Large	21	19	**40**
Total	**92**	**58**	**150**

TABLE 7. Ear signaling by size

	Ear Signal	No Ear Signal	Total
Small	28	3	**31**
Medium	59	13	**72**
Large	34	6	**40**
Total	**121**	**22**	**143**

TABLE 8. Tail signaling by breed type

	Tail Signal	No Tail Signal	Total
Working	25	25	**50**
Sporting	47	21	**68**
Herding	19	13	**32**
Total	**91**	**59**	**150**

TABLE 9. Ear signaling by breed type

	Ear Signal	No Ear Signal	Total
Working	41	9	**50**
Sporting	53	9	**62**
Herding	27	3	**30**
Total	**121**	**21**	**142**

TABLE 10. Ear vs. Tail Signaling

	Ear change			
Tail change	Forward	No change	Back	**Total**
Up	16	10	6	**32**
No change	29	4	19	**52**
Down	8	2	42	**52**
Total	**53**	**16**	**67**	**136**

TABLE 11. Tail and Ear Signaling by Size

		Tail change		
Ear change		Up	Down	**Total**
Forward	Small	2	0	**2**
	Medium	7	6	**13**
	Large	7	2	**9**
Back	Small	1	13	**14**
	Medium	3	23	**26**
	Large	1	5	**6**
	Total	**21**	**49**	**70**