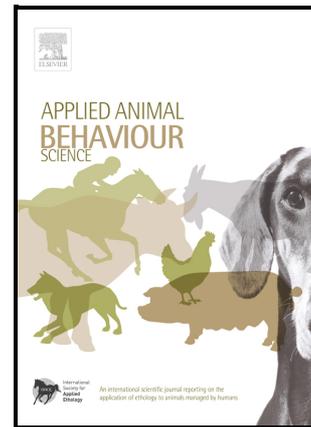


Ethogram of the predatory sequence of dogs (*Canis familiaris*)

Anna Broseghini, Miina Lõoke, Cécile Guérineau,
Lieta Marinelli, Paolo Mongillo



PII: S0168-1591(24)00250-8

DOI: <https://doi.org/10.1016/j.applanim.2024.106402>

Reference: APPLAN106402

To appear in: *Applied Animal Behaviour Science*

Received date: 9 July 2024

Revised date: 2 September 2024

Accepted date: 20 September 2024

Please cite this article as: Anna Broseghini, Miina Lõoke, Cécile Guérineau, Lieta Marinelli and Paolo Mongillo, Ethogram of the predatory sequence of dogs (*Canis familiaris*), *Applied Animal Behaviour Science*, (2024)
doi:<https://doi.org/10.1016/j.applanim.2024.106402>

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2024 The Author(s). Published by Elsevier B.V.

Ethogram of the predatory sequence of dogs (*Canis familiaris*)

Anna Broseghini, Miina Lõoke, Cécile Guérineau, Lieta Marinelli*, Paolo Mongillo

Department of Comparative Biomedicine and Food Science, University of Padua, Viale dell'Università 16, 35020, Legnaro (PD), Italy

Corresponding author's email and phone: lieta.marinelli@unipd.it +390498279418

ORCID:

Anna Broseghini: 0000-0002-8795-6237

Miina Lõoke: 0000-0002-3981-1551

Cécile Guérineau: 0000-0002-2283-1302

Lieta Marinelli: 0000-0003-0609-2172

Paolo Mongillo: 0000-0001-8599-4005

Abstract

Predatory behaviour is a relevant part of the behavioural repertoire of dogs, which often entails negative or desirable implications, depending on the context and target to which it is directed. It also considered one of the most characterising aspects of breed-specific behaviour. Despite its relevance, there is surprisingly little scientific knowledge about the topic. In the present study we sought to develop an ethogram of the predatory sequence of dogs, with the aim of providing a sufficiently general structure to be applicable to dogs at large, without eluding peculiar aspects of the species' specific behaviour. Sixty videos of dogs of different breeds expressing predatory acts, including both videos obtained from public internet repositories and videos made on purpose, were described in detail by two different observers. From descriptions, a general sequence was identified, consisting of four functional phases, i.e. search, approach, chase and bite. The descriptions of the behaviours included in each phase were organised into three levels, characterised by different levels of detail and focussing on different aspects of the behaviour. When appropriate, these descriptions highlighted differences in behaviour expressed by dogs belonging to different working groups. The ethogram

proposed in the present paper could represent a useful starting point for improving knowledge about the predatory behaviour of dogs and answering relevant questions about both its evolution and ontogeny.

Keywords:

Canids, ethological methods, hunting, predatory behaviour, prey

1. INTRODUCTION

An ethogram is an essential element in the study of animal behaviour. It is defined as the classification and the list of behaviours of a species, with associated definitions (Bateson & Martin, 2021). Ethograms come in many different formats, differing in the detail of information they provide, as well as in the criteria by which behaviours are classified. For example, different levels of characterisation can be found within or among ethograms, from the characterisation of a single motor act up to the identification of behaviours composed of complex motor patterns and even further to the identification of behavioural sequences. Moreover, it might also include the drawing representation or picture of the behavioural elements or sequence (McDonnell & Poulin, 2002; Strauss, 2006). Ethograms also vary in their degree of completeness. An ethogram can be exhaustive, in its absolute sense, when it provides the complete inventory of the behavioural repertoire of a species (Strauss, 2006). However, ethograms can also focus only on one category of behaviour or on a segment of the behavioural repertoire (Grier, 1984). Indeed, for scientific study purposes, it is much more common to concentrate only on the behaviour or behavioural categories needed for the research, hence producing a partial or working ethogram (Bateson & Martin, 2021). Regardless of these differences, one of the main characteristics that an ethogram should strive for is objectiveness, i.e., whatever is described must be traceable to the observed reality, excluding personal interpretations. For this reason, the descriptions of behaviours included in an ethogram should not focus on the proximate or ultimate causes of the behaviour, but only on the objective

description of postures/movements expressed during the given behaviour (Spagnuolo et al., 2021). Objectiveness is easily applicable when considering single motor acts. However, a complete ethogram also expects behavioural categories as behaviours are grouped into sets that are believed to serve a common purpose (e.g., foraging behaviours, reproductive behaviours, etc.) (Verrell, 1982). Yet, the function of behaviour(s) and the effect that the given behaviour has on the animal, other subjects and the environment should be included in an ethogram as a consequence of hypotheses on the function of the given behaviour (Brockmann, 1994). Therefore, it is necessary to concentrate on both the detailed description of a single behaviour/motor act and its functional description for a complete categorisation of behaviours.

Although ethograms are a widespread research tool, the lack of details and consistency in the description, classification and nomenclature of behaviours, often makes it difficult to compare reported results (Schleidt et al., 1984). The study of the predatory behaviour of large carnivores is an example of such difficulties (MacNulty et al., 2007). While for most other predators, predatory behaviour is divided into three well-defined units (i.e., search, pursue, and capture) (Holling, 1965; MacArthur & Pianka, 1966), for large carnivores, it is often generically referred as a whole 'hunt', with a lack of standardisation in terminology, classification, and interpretations (MacNulty et al., 2007). In the attempt to overcome these inconsistencies, MacNulty and colleagues observed the interactions between wolf packs and their prey to create a sufficiently detailed ethogram of predatory behaviour, possibly generalisable to other nearby species. The authors then compared their ethogram with other classifications and descriptions of the predatory behaviour of wolves and other large carnivores, determining a strong conceptual correspondence between them. Therefore, their ethogram was promoted as a general framework for comparing predatory behaviour within and between large carnivore species (MacNulty et al., 2007). As a result of the work of MacNulty and colleagues, the sequence of wolves' predatory behaviour was formalised as 'Search-Approach-Watch-Attack-Capture'.

Among canids, not only the predatory behaviour of the wolf has been described, but also that of coyotes (*Canis latrans*) (Wells & Bekoff, 1982;), African wild dogs (*Lycaon pictus*) (Creel & Creel, 1995; Estes & Goddard, 1967;), foxes (*Vulpes vulpes*) (Henry, 1986; Lloyd, 1980) and jackals (*Canis aureus*) (Moehlman, 1987). When it comes to dogs (*Canis Familiaris*), research on predatory behaviour has been surprisingly very limited. However, predatory behaviour still represents an important aspect of the behavioural repertoire of dogs, and the expression of predatory behaviour of dogs can have important consequences, (McLennan, 2023), especially considering the great diffusion of this species. The impact of free-ranging/feral dog predation on the ecology of wild fauna is well reported in the literature. For example, Manor and Saltz reported that free-roaming dog predation was the major factor affecting the rate of increase in the gazelle population (*Gazella gazella*) along the southern coastal plain of Israel, contributing to its decline (Manor & Saltz, 2004). In an Iberian semiarid shrub steppe, incidental predation by feral dogs seriously affected the conservation of rare steppe larks (Yanes & Suárez, 1996). Also, companion dogs can have an impact on wildlife. A single female German Shepherd was responsible for killing more than half of one of the largest kiwi populations in New Zealand (Taborsky, 1988). Lenth and colleagues found that several wild species changed their patterns of habitat use and activity due to the presence of pet dogs along recreational trails (Lenth et al., 2008). Not only can wildlife be affected by predatory acts expressed by dogs, but also farm and other companion animals. Emblematic is the case of a 2-year-old German Shepherd who killed dogs, cats, hens, and rabbits living nearby, with a presumptive diagnosis of 'predatory aggression' associated with 'territorial and protective aggression' (Chávez & Opazo, 2012). During the analysis of 245 cases of aggressive behaviour by dogs, Borchelt identified predatory aggression toward other small animals as one of the main types of aggression observed (Borchelt, 1983). Furthermore, aggressive attacks by dogs on other dogs are often reported to display characteristics that strongly resemble predatory behaviour (Schilder et al., 2019) and the same has been suggested in aggressive attacks by dogs towards humans (Borchelt, 1983).

Despite the negative consequences reported above, the predatory behaviour of dogs was and is widely sought after in work contexts. As a result, hunting dog breeds are required to perform specialised behaviours, including chasing, holding at bay, pointing, retrieving, flushing, following a smell trail or the blood trail of a wounded animal (Ridgway, 2021). Breed differences in the repertoire of predatory behaviours of dogs have only been explored by very few studies.

Christiansen and colleagues investigated behavioural differences among three breeds of hunting dogs while confronting a potential prey, finding elkhounds having the highest interest, initial hunting motivation, percentage and severity of attacks (Christiansen et al., 2001). To the best of our knowledge, only Coppinger and collaborators provided a tentative description of dogs' predatory sequence. In their work, they suggested that dogs bred for different functions present specialised behaviours originating from an ancestral sequence, formalised as orient-eye/stalk-chase-grab bite-kill bite-dissect-consume (Coppinger et al., 1987; Coppinger & Coppinger, 2002). Breed-typical predatory sequences would be the result of selective enhancement or inhibition of specific motor patterns of such sequence. For instance, in several breeds the killing bite would have been inhibited, to prevent dogs from ruining the prey's carcass. This assumption finds some support by the observation that Beagles do not kill their preys, as opposed to coyote or coyote x Beagle hybrids, with a sequence truncated after the grab-bite phase (Fox, 1976). However, for most of it, Coppinger's hypothesis remains unverified, in terms of the behaviours that comprise the sequences of ancestral and modern breeds. Also, Coppinger's sequence appears to be built around behaviours that are highly breed-specific and certainly not applicable to all dogs. However, similar postulations about dog predatory behaviour and differences in terms of behavioural sequence between dog breeds have been assumed to be true by the public, professionals and researchers (Gadbois et al., 2015; Mehrkam et al., 2017; Udell et al., 2014).

Under these premises, the present study aimed to develop a detailed descriptive characterisation of the behaviours expressed in dog's predatory sequence, using both videos obtained on the Internet and videos specially made for this aim. Given that this is the first detailed characterisation of a dog's

predatory sequence, it was crucial to observe the behaviours within an unequivocal predatory context, avoiding both behaviours that might resemble predatory actions but occur in non-predatory contexts, and potentially predatory behaviours that could represent modifications of the predatory sequence induced by selective breeding for tasks other than hunting, such as herding or guarding. To provide a preliminary evaluation of behavioural consistency within and among dogs' working groups, the observations were made in representative dog hunting breed, possibly revealing the existence of behavioural variants of predatory sequence in different groups of hunting dogs.

2. MATERIALS AND METHODS

The procedure for the obtainment of the ethogram of the predatory sequence involved several steps, summarized as follows, and described in detail in sections 2.1 - 2.5:

1. the collection of videos of dogs expressing predatory behaviour
2. the definition of a presumptive functional predatory sequence
3. the thorough and detailed objective description of the behaviours expressed by dogs in the videos
4. the verification of the applicability of the presumptive sequence and, if needed, the modification of the sequence to adapt it to the observed behaviours
5. the organization of the description of the sequence into levels with different aims and detail.

2.1 Video selection

The first step of the procedure was the selection of videos that clearly demonstrated predatory behavioural patterns, which eventually consisted of sixty videos, of which forty-five obtained from the Internet and fifteen were filmed *ad hoc*.

Videos obtained from the Internet were part of a pool of about six hundred videos found on YouTube using the keywords 'dog' 'chase/chases/chasing' 'hunt/hunts/hunting' 'catch/catches/catching'. Provided that the videos had good image quality, a subset was selected for

analysis, requiring that the dog clearly expressed predatory behaviours, by fulfilling the following criteria:

1. being filmed in a natural setting (i.e., not in urban areas, at home or in the backyard);
2. showing the dog unleashed or, at most, with a long leash left loose on the ground;
3. the description and/or title of the video identified the video as displaying a hunting context;
4. displaying at least two behavioural patterns commonly associated with predatory behaviour, according to descriptions found in the literature and common sense;
5. showing the capture or attempted capture of a live prey by the dog.

The requirement to identify at least two of these behaviours (criterion 4), along with the other selection criteria, provided a conservative and precise method for including videos in our sample. This ensured that we were accurately describing predatory behaviours rather than predatory-like behaviours (e.g. chasing observed in play contexts).

To increase the number of videos representing the early phases of the predatory sequence, the selection of videos was later expanded, including those that met the first four criteria but not necessarily the last one.

The fifteen videos made *ad hoc* were opportunistically recorded during hunting activities in an open field. The participants were hunting dogs, which, during the activity, were left free to search, locate, chase and bite the prey without any indications or commands from the owner. The videos were filmed with a Canon XA20 camcorder (Canon, Tokyo, Japan).

2.2 Definition of a presumptive predatory sequence

We initially defined a presumptive predatory sequence, which suitability to describe dogs' predatory behaviour would be subsequently verified. A required characteristic of the sequence was that its phases should have been general enough to accommodate differences in behaviours expressed by dogs of different breeds. Therefore, rather than representing specific behaviours which might not be shown by all dogs (e.g. point, stalk, etc.), phases of such presumptive sequence had to represent

functions which any predatory act would normally encompass. A similar rationale had been adopted before to describe a predatory sequence for wolves and large carnivores (MacNulty et al., 2007) and we therefore initially adopted the five functional phases therein reported: search, approach, watch, attack, capture.

2.3 Observation and description of the behaviour expressed by dogs

Phases of the abovementioned presumptive sequence was used to divide the videos into subparts. Two independent observers were assigned to each phase, describing in detail the content of all the videos from their assigned phase. The observers described the behaviours using a table that listed all the potential movements and postures a dog might exhibit, which was necessary to capture all possible behavioural patterns (Table S1). To ensure accuracy, the observers were initially trained with the process by using the table to describe dogs' behaviours from videos unrelated to predation. Information collected in the descriptions concerned: the context in which the event was taking place, the group of the dog according to the Fédération Cynologique Internationale (FCI), what happened before and after the phase, the characteristics of the prey, the general and local posture and movement displayed by the dog, and, for the biting phase, the characteristics of the bite. When the quality and content of the video allowed it, a more detailed description was carried out on the dog's sensory orientation. The two descriptions were compared to assess consistency and to identify possible details noticed only by one of the observers. In the event of disagreement between the two descriptions, a third independent observer, unaware of the other two descriptions, described the video for a final agreement.

2.4 Verification of the applicability and modification of the sequence.

Confirmation of the applicability of the presumptive sequence implied verifying that all behaviours observed could unequivocally be attributed to one of the phases, that all the phases were represented and clearly distinguishable and that the general behaviour showed consistency across individuals.

Two phases of the sequence that we had initially identified could not be clearly distinguished, namely *approach*, defined as to reduce distance and to decide whether to attack the prey, and *watch* which refers to prey assessment. Since the dogs' behaviour generally fitted with both functions, we eventually opted to merge them into a single 'approach' phase.

Moreover, the phases originally labelled as 'attack' and 'capture' were renamed 'chase' and 'bite'. The terms 'attack' and 'capture' seem to be more appropriate for large wild carnivores, as they often involve complex and coordinated group hunting strategies. While the function of these phases remains similar to those in large carnivores, we found it more appropriate to use terms that are more commonly applied to domestic dogs in both literature and applied fields. Moreover, these terms seemed to us more neutrally describe the functions of each phase.

As a result, the final predatory sequence was composed of four phases: search, approach, chase and bite.

2.5 Organization of sequence descriptions

The description of the sequence's phases was organised into three different levels with progressively increasing detail. Level 1 provided a general description of the phase, including potential external triggers or evident change in behaviour that determine the onset and the end of the phase. Level 2 described the dog's locomotion, including gaits and direction of movements, postures, including centre of gravity, limbs, trunk and head alignment, and the description of specific local states/events, including position and movements of the tail, degree of mouth opening, presence of muscular tension/tremors and urination or defecation. Level 3 described sensory orientation, including head and eye orientation, presence of olfactory exploration associated or not with nostril movements, position and movements of the ears, and vocalisations.

3. RESULTS

The dog breeds represented in the 60 videos belonged to 3 working groups, for which it was possible to find a relatively large number of subjects: 34 Pointing dogs (FCI Group 7), 13 Scent hounds (FCI Group 6), 13 Sighthounds (FCI Group 10). Only a handful of other videos were found representing other – albeit popular – hunting dog breeds (Dachshund N = 1, Retriever N = 2, Terrier N = 2), which responded to the selection criteria. These videos were excluded from further analysis, for the low number of subjects per breed made it impossible to effectively identify potential behavioural within breed consistencies.

The observation of the videos resulted in 146 descriptions. Of these 35 referred to the search phase, of which 14 allowed detailed collection of facial and sensory characteristics during the phase, 43 to the approach phase with 10 allowing collection for the facial and sensory characteristics, 38 to the chase phase of which 8 included the facial and sensory characteristics collection, 30 to the bite phase with 6 allowing facial and sensory characteristics collection.

For phases in which qualitative differences in behaviours were observed between dog groups, descriptions are provided separately.

Regardless of grouping, the phases of the sequence generally occurred in the order described. However, not necessarily all phases were always expressed (Table 1). In some cases, the sequence was interrupted before completion, for instance if the prey escaped before a grab-biting attempt could be made or if it remained motionless, as further discussed below. The approach phase was also a potential point of interruption, as in some cases the dogs interrupted the approach and reinitiated the sequence from the search phase.

Table 1. Number of times each phase was observed in each of the three dogs' group, relative to the total number of videos in which the phase could have been observed, i.e. the videos were not truncated after the beginning or before the end of the sequence.

	Search	Approach	Chase	Bite
Pointing Dogs	23/23	24/27	17/19	14/17
Scent Hounds	12/12	12/12	10/10	5/9
Sighthounds	0/0	7/7	11/11	11/11

3.1 SEARCH PHASE

This phase was observed in pointing dogs and scent hounds, hunting live birds hidden in the grass or bush or hares/rabbits. This phase was not observed in sighthounds. The apparent function of this phase is to detect sensory cue of the presence of the prey in the surrounding without clear orientation towards a specific area of the environment.

Other names: Orient (Coppinger & Coppinger, 2002); Locate (Ridgway, 2021); search, tracking (Schmutz & Schmutz, 1998); search (Lehner, 1976; MacNulty et al., 2007; Wells & Bekoff, 1982); travel in search (Creel & Creel, 1995); hunting drive (Arvelius & Klemetsdal, 2013); hunt (McLennan, 2023).

3.1.1 Pointing dogs

Level 1 - General description

This is an exploratory and dynamic phase in which the dog is attentive to a wide portion of the environment.

The dog moves quickly, covering large areas, with a changing/unprecise direction. As the search phase is characterised by olfactory/visual exploration (see details at section 3.1.1), transition to the

next phase occurs when the dog apparently intercepts a sensory cue of the prey. The transition occurs abruptly, or in a progressive fashion, with a clearer directionality of the movements and a gradual reduction in speed, until the dog completely stops.

Level 2 - *Body Posture and Movement*

During the first part of the phase the dog moves quickly through the environment, displaying mostly zigzag patterns of direction, with running gaits (gallop or canter). Direction changes are initiated by the head, followed by the rest of the body. The centre of gravity tends to be centred with extended limbs.

As the phase progresses the range of lateral movements tends to decrease, although the head may still show wider latero-lateral rotations than the body. The gait tends to slow down to trot or walk and a slight flexion of the limbs can be observed. The head may begin to be stretched forward forming a single linear plane with the trunk. The transition to slower and more controlled movements is accompanied by an increase in sensory orientation and body stiffness, even if no muscle tremors are evident.

Throughout the phase, the trunk is straight and parallel to the ground. The head is higher or lower than the trunk line depending on where the olfactory cue is located (i.e., range from ground to up in the air) and on the characteristics of the environment where the dog is searching (e.g., in the presence of physical obstacles the dog will tend to hold its head up). The tail is held along, under or above the trunk line presenting a very rapid and shallow tail wag, with lateral and/or circular movements. Rarely, the tail did not show any wagging. The mouth of the dog is open when the dog is not sniffing. This is the only stage of the predatory sequence where urination/defecation can be observed.

Level 3 - *Sensory orientation and vocalizations*

Searching phase is characterised by the presence of visual and olfactory exploration of the environment, evident by both lateral and vertical head movements accompanied by sniffing the air and/or the ground. Sometimes nostril movements can also be observed. Ears are either neutral, held backward or lifted sideways. Toward the end of the phase the ears may begin to be held forward. Vocalisations were absent.

3.1.2 Scent Hounds

Level 1 - *General description*

As this type of dog usually hunts in groups, the behaviours identified and described refer to a group of dogs (minimum 2), which may therefore influence each other. It is an exploratory and dynamic phase where the initial search pattern presumably aims to find the olfactory trail of the prey. The dog inspects the ground without a precise direction, apparently working independently of the others, each inspecting one zone and continually moving to others, not necessarily adjacent to each other. The phase ends when the dogs find a useful trail of prey that they start to follow.

Level 2 - *Body Posture and Movement*

The dog sniffs the ground, either being stationary or moving with a walking gait or at trot. Alternatively, the dog lifts its head off the ground and moves away to start sniffing a new area. In these cases, the gait is faster, cantering and/or galloping, the centre of gravity is centred, and limbs are extended. When the dog is sniffing the ground, its centre of gravity is still centred but with a forward inclination of the trunk, with slight flexion of the front limbs. The head, in line with the trunk line, is very close to the ground. The tail is along or above the trunk line presenting a rapid and shallow wag, with lateral and/or circular movements. Rarely the tail does not wag. The mouth is always closed when the dog is sniffing but can be either open or closed when not sniffing. This is the only stage of the predatory sequence in which urination/defecation can be seen.

Level 3 - Sensory orientation and vocalizations

This phase is characterised by the presence of an olfactory exploration of the environment, which is evident as the dog's head is mostly attached or closer to the ground. Nostril movements are observed and the sound of sniffing and blowing air is audible. Ears are either laterally relaxed or lifted sideways. Dogs can bark, but barking becomes frequent and intense as the sequence goes on.

3.2 APPROACH PHASE

This phase was observed in pointing dogs, hunting live birds hidden in the grass or bush, in scent hounds, hunting hares/rabbits, and in sighthounds, hunting hares/rabbits. The presumed function of this phase is to get closer to the localized prey to catch it.

Other names: eye and stalk, forefoot stab (Coppinger & Coppinger, 2002); locate, pointing (Ridgway, 2021); pointing, pounce (Akkad et al., 2015); pointing (Schmutz & Schmutz, 1998); orient, stalk, walk, pounce (Wells & Bekoff, 1982); approach, stalking attitude (Estes & Goddard, 1967); approach, watch (MacNulty et al., 2007).

3.2.1 Pointing dogs**Level 1 - General description**

In this phase the dog displays two behaviours: an immobile stance (commonly known in the hunting world as pointing), and a slow and controlled locomotion (commonly known as stalking). At the end of the previous phase, pointing is displayed; the transition from search to pointing seems to be elicited by the detection of the prey in the nearby. Stalking is displayed only after pointing has taken place. However, after the first instance of pointing, alternations of pointing and stalking can occur henceforth. There are no evident external events or stimuli that determine the onset of stalking after

pointing and vice versa. This phase ends when dogs are sufficiently close to the prey and chasing/lunging starts. In the few cases where the prey does not flee, the dog can express directly teasing behaviours, which include:

- Staring: the dog stares at the prey, with the tip of the nose from about half a meter to touching the prey with its nose.
- Touching with a paw/s: the dog uses one front paw at a time to touch the prey. The touch can be both gentle and firm.
- Snapping: the dog withdraws its neck toward the body and then snaps it forward to muzzle the prey.
- Stiff legged jump: the dog moves its weight on its hind legs, lifting on its hind legs, and then slamming both front limbs, held straightened and rigidly, to the ground on or close to the prey.

Potential functions of these behaviours include assessing the prey's reaction, stunning the prey to bite it, or setting it in motion to start chasing.

Level 2 - Body Posture and Movement

Both pointing and stalking encompass a constant body orientation toward the prey. In the case of pointing, the dog is in a quadrupedal, stationary stance with evident body muscle tension. Often a fore or hind limb is raised, from only a few centimetres off the ground to maximal flexion of all the limb joints, with the paw close to the trunk/abdomen. During stalking, the dog moves toward the presumed location of the prey by raising one paw at a time close to the trunk/abdomen, before placing it down on the ground. Stalking is a 4-step, diagonal gait, initiating with either a front or hind limb (e.g., front-right, hind-left, front-left, hind right). It can be characterised by various speeds, from very slow to faster gaits. Sometimes the increased speed of stalking is associated with more frequent and wider head movements, possibly related to sensory exploration (see Level 3).

The centre of gravity can be either centred or forward. The limbs can be extended or flexed ranging

from a slight flexion to almost full flexion. Lowering generally occurs rapidly as soon as the dog starts the behaviour, and it remains henceforth constant as long as that behaviour is expressed. Further lowering of the posture may or may not occur at any subsequent transition between pointing and stalking, and vice versa. Therefore, throughout the phase, the dog can adopt the final height of the posture at the first expression of the behaviour and keep it constant or lower its posture with decreasing distance from the prey. During pointing, the trunk can be straight and parallel to the ground, or not, depending on the alignment of the trunk at the moment of detection of the prey. If not, the trunk is straightened as soon as the stalking locomotion starts. The head is kept above or in line with the trunk. In most cases, it is extended forward, and it is generally immobile, except in specific situations described in Level 3. The tail is held along, above or below the trunk line and it is still and stiff. It is common to observe tail, trunk, neck and head aligned to form a single linear plane, which is more evident when the posture is lowered. The mouth tends to be either closed, opened for a short time and immediately closed again, or kept always open; in this latter case the dog does not appear to be panting but rather shows very controlled respiratory movements. Muscle tremors can be seen in the limbs, tail and neck area.

During teasing behaviours, unlike pointing/stalking, the dog is stationary on the prey or moves around it. The posture is low, even to complete the sternal decubitus. The dog's neck is stretched forward, and the head is kept below the trunk line, close to the ground and the prey. The dog wags its tail conspicuously, making quick lateral tail movements. The mouth is closed and sometimes the dog sticks its tongue out with or without licking its upper lip. The dog does not seem to have the same body stiffness that it does during pointing/stalking-

Level 3 - Sensory orientation and vocalizations

The approach phase is characterised by the presence of constant sensory orientation toward the prey. The head is fully orientated in the direction of the presumed location of the prey and does not displace, except for rare and brief diversions to look at distractors. The eyes are usually turned in

the direction of the prey. Nostril movement generally occurs with the mouth closed and the nose orientated in the direction of prey. If the dog has the mouth open, dilation of the nostrils can also be observed when the dog closes the mouth for brief moments. Sometimes, the dog makes quick, narrow and controlled sideways or downwards head movements, associated with movements of the nostrils. This behaviour seems to be expressed when the dog loses the scent trail and needs to re-intercept it. Ears are either neutral, lifted sideways or held forward. Vocalisations are absent. During teasing behaviours, the dog is oriented towards the prey even if its attention does not appear to be as intense and constant on the prey as it was during earlier stages of the predatory sequence. Nostril movements can be present. The dog's ears are fully turned forward toward the prey.

3.2.2 Scent Hounds

Level 1 - *General description*

This phase presents behavioural patterns like the previous search phase but more precisely oriented. The phase starts when the dog apparently finds the olfactory trail of the prey. The dogs begin to follow the trail with a clearer directionality, and it is notable that every dog is moving linearly in the same direction. This can last for a long time and over long distances, and it is common for dogs to alternate this phase with the previous search phase, as they apparently lose the olfactory trail or its directionality. This is generally accompanied by increased excitement and an increase in frequency of vocalisations, compared to the previous phase. The phase ends when the dog reaches the prey and scouts it out. This moment is characterised by the culmination of the states of excitement, with an incessant and shrieking barks.

Level 2 - *Body Posture and Movement*

The dog usually sniffs the ground, either being stationary or moving with a gait, ranging from walk to trot or even canter. Sometimes, the dog lifts its head off the ground and moves forward. In these

cases, the gait is faster, cantering and/or galloping, the centre of gravity is centred, and limbs are extended. When the dog is sniffing the ground, its centre of gravity is still centred but with a forward inclination of the trunk, with slight flexion of the front limbs. The head, in line with the trunk line, is very close to the ground. The tail is along or above the trunk line presenting a rapid and shallow wag, with lateral and/or circular movements. Rarely the tail does not wag. The mouth is always closed when the dog is sniffing but can be either open or closed when not sniffing.

Level 3 - *Sensory orientation and vocalizations*

The approach phase is characterised by the presence of olfactory exploration of the environment, which is evident as the dog's head is mostly attached or closer to the ground and moved along a trail, sometimes showing lateral zig zag displacement and going back and forth over the same section of trail even several times. Nostril movements are observed and the sound of sniffing and blowing air is audible. Ears are either laterally relaxed or lifted sideways. Barking is present, becoming more frequent and of higher pitch as the phase goes by.

3.2.3 Sighthounds

Level 1 - *General description*

In the approach phase the dog pays close attention to a specific area of the surrounding, as if expecting an imminent detection of prey. Visual exploration is evident but limited in space. The dog can either move forward aiming to get as close as possible to the area where the prey is assumed to be or stop/stand still when the latter has been reached. The phase ends as soon as the movement of the prey sets the dog off on chase.

Level 2 - *Body posture and movement*

When the dog moves, the gait is usually trot, following a straight direction. When the dog is stationary, and the prey has not started fleeing, it may exhibit flinches that seem to anticipate the initial burst of chasing. The centre of gravity is centred, and the posture is with extended limbs. When the dog is moving, the trunk is straight and parallel to the ground, while when the dog is stationary the trunk can also be slightly leaning forward if the dog is paying attention to a specific area/den. As a result, the head is held either higher or in line with the trunk. Rapid, latero-lateral movements of the head are generally present, although the dog can focus on a specific area, not showing any head movement. When the dog moves, the tail is held higher than the trunk line showing a quick lateral wag, while when the dog is still, the tail is lower than the trunk line and still. The mouth can always be closed, open when the dog moves, and closed when the dog stops.

Level 3 - Sensory orientation and vocalizations

The head is rotated with lateral movements, allowing the dog to visually scan the environment, and the ears position can range from forwards to backward; they can be motionless or presenting forward, sideways and backward rotations (the two ears do not necessarily move consistently). Generally, if the dog is moving and stops to focus on a specific area, or if it flinches when it is already stationary, the ears are brought forward. No nostril movements are observed. Vocalisations are absent.

3.3 CHASE PHASE

This phase was observed in all working groups of dogs hunting live birds and hares/rabbits. The function seems to further reduce the distance from the prey, allowing the dog to grab the latter.

Other names: Chase (Coppinger & Coppinger, 2002); chasing (Ridgway, 2021); attack, pursuit, chase (Creel & Creel, 1995); rush (Wells & Bekoff, 1982); attack (Lehner, 1976); chase (Estes & Goddard, 1967); attack (MacNulty et al., 2007).

3.3.1 Pointing dogs, scent hounds, sighthounds

Level 1 - *General description*

Chasing is a quick locomotion that takes the dog at biting distance from the prey. Just before chasing, the dog can be expressing different approaching behaviours (i.e. searching, pointing/stalking/teasing behaviours) depending on the type of dog and behaviour of the prey. In fact, chasing is elicited by the sudden movement of the prey escaping. Chasing ends with an extension of the neck and head towards the prey and the attempt to grab it. If the dog gets close enough to the prey before starting an actual chase, the dog can just make a quick leap forward (lunging). If by doing this, the dog fails to capture the prey, lunging may turn into chasing.

Level 2 - *Body posture and movement*

In this phase, the dog moves quickly, in a galloping gait. The centre of gravity follows the kinetics of movement during chasing and tends to shift forward when the prey is close enough to attempt grabbing it. The trunk is not always straight and parallel to the ground. Variations in trunk position and head position depend on prey behaviour and distance. The tail can be along or below the trunk line. Lateral and/or circular movements can be observed when the dog expresses lunging behaviour or when the dog performs a rapid change of direction because of a sudden change in the direction of the prey (e.g. with hares or rabbits, whose run is characterised by many rapid changes of direction). In both cases tail movements occur at the moment of maximum proximity to the prey. The mouth can be either closed or open, in some cases anticipating a bite.

Level 3 - *Sensory orientation and vocalizations*

The orientation of the dog during chase is kept towards the prey, with the head fully orientated in the direction of the moving prey. Ears in pointing and scent hounds seem relaxed, moving in

accordance with the run, or are held backward. Sometimes the ears can be held forward during the first lunge towards the prey. In Sighthounds, ears are held backward, in most of the observed cases, or forwards. Vocalisations are not emitted except for scent hounds, which show frequent shrieking barks throughout the phase.

3.4 BITE PHASE

This phase was observed in dogs of all working groups hunting live birds (in most cases shot down) and hares/rabbits (directly captured by the dog or shot by hunter). The function of the first bite is to catch the prey and land it still or keep it on the ground. After the first bite, subsequent acts on the prey can happen and have variable functions and characteristics, therefore, the descriptions in the below levels refer only to the first bite, while what happens next is described in the below section 'Other types of bites'.

Other names: Grab bite, kill bite, head-shake, dissect (Coppinger & Coppinger, 2002); retrieve (Ridgway, 2021); sustained grabbing, holding, shaking, tearing (D'Ingeo et al., 2021); head-thrust, crush-bite (Wells & Bekoff, 1982); capture (Lehner, 1976); capture, disembowelment, killing (Creel & Creel, 1995); capture, killing, grab, pull, tear apart, dismemberment (Estes & Goddard, 1967); capture (MacNulty et al., 2007), possess (McLennan, 2023).

3.4.1 Pointing dogs, scent hounds, sighthounds

Level 1 - General description

Biting behaviour occurs when the dog is close enough to the prey to expect to catch it, usually following chasing or lunging behaviour.

Level 2 - Body posture and movement

The postures expressed during the capture bite depend greatly on the behaviour of the prey. The dog starts biting while still in motion. In case the prey is motionless (e.g. shot by the hunter), the dog's movement and posture are in accordance with the braking, with the front part of the body stopping on the prey, while the rear is pivoting, following the chasing inertia. If the prey is fleeing, posture and movement seem to be aimed at either not letting the prey slip out of its mouth or catching it more firmly and finally landing it on the ground. The prey is usually bitten in the middle or back part of the body and once it is on the ground, the dog assumes a centred centre of gravity. The trunk is straight, with the head lowered, or bent forward on the prey, with the head aligned with the trunk. The hindlimbs are generally more extended than the forelimbs. The tail is kept in line with the trunk or higher and it can be motionless, although not rigid, or it can move in a very rapid and shallow tail wag, with lateral and/or circular movements. The mouth is engaged in the bite.

Level 3 - *Sensory orientation and vocalizations*

During the capture bite the dog's attention is still always directed toward the prey, showing a clear and constant sensory orientation on it. Ears are either neutral or held backward. Vocalisations are absent.

Level 3.1 - *Other type of bites*

During subsequent bites, the dog's attention is usually on the prey, although the sensory orientation does not appear to be as intense and constant as it was in the capture bite and earlier stages of the predatory sequence.

Assessment bites: The function of this behaviour could be to assess the state of the prey and to ensure that it is dead, but not to ingest/dissect the prey. It could also be performed because chewing is a satisfying activity for dogs, fulfilling behavioural needs (Arhant et al., 2021). The dog delivers repeated and rapid bites on the prey. It tends to do this by holding the prey on the ground with the paws, and leaning over it, assuming a position like bowing. Therefore, the trunk is tilted forward,

the head along the trunk line, forelimbs are flexed, and hindlimbs are extended, thus the back can be either arched or kyphotic. The dog can also exhibit these bites by lifting the prey off the ground, showing a straight trunk parallel to the ground, head held above the trunk line and limbs extended. The tail can be kept along, higher or lower the trunk line and be motionless or, as in most cases, moved in a lateral and rapid wagging. Ears are neutral or backward. The prey is bitten in the middle part of the body, between the wings for birds and on the back for hares.

Tug bite: The function of this bite could be to keep the prey for itself, preventing/limiting access to other dogs. The prey may be bitten simultaneously by two or several dogs who lift it off the ground and tug at it, each pulling one end of the animal. Tugging can occur with the dogs stationary in place, pulling in the opposite direction, or moving in the same direction on a trot gait. A brief head shake bite (see section 3.4.1) can be observed during this behaviour. The dogs have a straight trunk parallel to the ground, head held above the trunk line and limbs extended. The tail can be kept along or higher the trunk line and be motionless or moved in a lateral and rapid wagging. The dog's attention is both on the prey and on other/s dog/s.

Head shake bite: The main function of the head shake bite appears to be to kill the prey. The dog shows a shaking movement of the head while holding the prey in its mouth. The movement is very intense and rapid and follows a "8" pattern in the horizontal plane. The head shake is performed in a stationary or moving position, with a straight trunk parallel to the ground, head above the trunk line and limbs extended. The tail is kept along or higher the trunk line and moves in an uncoordinated manner as the whole body is shaken by this bite. The position of the ears follows the intense and fast movement of the dog's head. The prey is bitten and held in the neck/scapular area or back part of the body.

Retriever bite: This type of behaviour has been observed in pointing dogs. The function of this bite is to bring the prey back to the human figure of reference. After capturing the prey, the dog holds it firmly in its mouth and heads back to the handler. The dog may exhibit this behaviour spontaneously, or after a signal/command by the handler. While showing this behaviour, the dog

canthers, displaying a posture as high as normal, the centre of gravity is centred, the trunk straight and parallel to the ground, with the head higher. The tail is held along the trunk line and can be held still (except for movement dictated by gait) or present a fast wag. Ears are neutral or held backward. The prey is bitten in the middle part of the body, generally between the wings for birds and on the back for hares.

Dissect bite: This type of bite has not been observed.

4. DISCUSSION

The aim of this work was to provide a detailed and structured description of dogs' predatory sequence, regardless of their hunting specialisation. Our proposed sequence encompasses four phases, i.e., searching for the prey, approaching it, chasing it and (attempting to) capture it, which were applicable to dogs of different working groups, supporting the suitability of such division. Other choices could have been possible, although they seemed less appropriate. For instance, in the scientific literature on other predators, predatory behaviour is often subdivided into search, pursue, and capture (Holling, 1965; MacArthur & Pianka, 1966), thus not considering an approach phase. However, in dogs, such a phase has both an identifiable aim – getting as close to the prey as possible before chasing – and distinctive behaviours, which clearly distinguish it from the search phase. This seems to apply especially to some dog breeds, such as scent hounds, where the approach phase entails a clear linearity of movements and increased bark frequency compared to search, or pointing dogs, where approach is uniquely characterised by pointing and stalking. Therefore, not including an approach phase in the predatory sequence of dogs would have implied losing a highly characteristic and specialised part of the predatory sequence. On the other hand, including more phases – as done by other authors – also seemed inappropriate. For example, it was suggested that a predatory sequence for wolves and large carnivores should include between approach and chase a 'watch' phase, aimed at assessing prey (MacNulty et al., 2007). However, we

did not observe behaviours specifically aimed and restricted at such a function in the predatory acts we observed. A possible exception could be represented by the ‘pointing’ behaviour of pointing dogs; however, as this frequently alternates with stalking, and sometimes the latter, rather than pointing, precedes chasing, pointing does not seem to represent a standalone phase.

Overall, we believe that our proposed sequence could fit the description of dogs’ predatory acts, being sufficiently general to be applicable to dogs at large, without eluding the peculiar aspects of the species’ specific behaviour. Moreover, the use of functional phases and the overall similarity of the sequence would be suitable for comparisons with canids or other carnivores, in line with ideas proposed by MacNulty and collaborators (MacNulty et al., 2007).

The level of detail provided by ethograms can vary remarkably (Okada et al., 2007 for a very detailed description and Seremak et al., 2023 for a less detailed one), depending on both the amount of available information and the intended usage scenarios. The case of dogs is unique among animals, since knowledge about the behaviour of the species is used at different levels, including pet ownership, breeding, training, veterinary healthcare, and various fields of research. For this reason, we opted to layer the description of the behaviours expressed in the sequence on three levels, differing in both focus and level of detail. Specifically, the first level provides a general description, which broadly highlights what behaviours are expressed within a phase and what triggers their onset and termination, whereas less emphasis is placed on the morphology of the behaviour itself. We believe that this level could be useful in the context of ecological or comparative studies, where the focus is more likely to be on the relationship between the animal behaviour and the surrounding (e.g. environment, prey, competitors, group members), rather than on the details of the behaviour itself. On the contrary, most details on how behaviour is expressed, including gaits, postures, position, and movement of specific body parts, are provided in Level 2. This descriptive layer could be particularly useful when analysing individual differences, for instance, in the context of training and breeding or characterisation of breed-specific behaviours. The third level of description includes local details, mostly focussing on sensory orientation. We

consider this level of detail relevant for research on mechanisms underlying the expression of predatory behaviour, including the perception and recognition of stimuli and the ability of the latter to attract and hold dogs' attention.

Both the overall sequence and the behaviours expressed by dogs within phase showed high consistency within breeds, with variability apparently elicited by prey-related factors. For instance, in few cases dogs found themselves close enough to the prey during search, resulting in the absence of an approach phase, the teasing behaviour was only observed if the prey remained immobile upon being reached and biting was obviously not observed if the chase was unsuccessful in taking the prey within dogs' reach. As for comparisons between breeds, there was, as expected, much more variability, and the largest differences were observed in the type of behaviours expressed during search and approach. A proper search phase was not observed in sighthounds. The visual exploration observed in these dogs was generally restricted to a specific area and accompanied by body tension and reactivity – it immediately preceded the setting off into chase – which were all consistent with the definition of the approach phase. It should be noted, however, that in the sighthound videos we found, it seemed clear that dogs were taken by handlers to a location where prey location was expected or already known by dogs. Thus, our results do not negate that a search phase would be expressed by sighthounds, in the lack of pre-existing expectations of prey location. In both pointing dogs and scent hounds the search phase was clearly defined, encompassing in both breed groups the exploration of variable wide portions of the environment with frequent changes in direction. Sniffing was observed in both groups, although often directed at air-borne odorants in pointing dogs, in line with the odour dispersion fluctuating plume model (Gifford, 1959).

Conversely, olfactory exploration is almost always directed toward the ground in scent hounds. This marks a discrepancy with the sequence proposed by Coppinger and collaborators (Coppinger & Coppinger, 2002), where the first behaviour – orient – does not entail any olfactory search. Such behaviour is defined as characterised by head above the shoulders, ears up, eyes and nose focused on the potential prey item (Lord et al., 2016), resembling what we observed at the end of the search

phase and onset of approach in pointing dogs, but not in scent or sighthounds. However, this variety of behaviours and sensory exploitation shown by dogs in the search phase is unsurprising, considering that wolves can use multiple modalities to find preys, including tracking, scenting and sighting (Peterson & Ciucci, 2003).

The largest variability in behaviours was observed in the approach phase. Pointing dogs showed characteristic alternations of pointing and stalking behaviours. These behaviours closely correspond to Coppinger's descriptions of the eye and stalk, respectively (Coppinger & Coppinger, 2002; Lord et al., 2016). However, based on the observations performed in the present study, two behaviours are not necessarily sequential, as they frequently alternate and any of the two can follow the search phase or precede the chase; moreover, there is clear qualitative consistency between the two, which seem solely differentiated by the presence/absence of locomotion. Due to this, we propose that the two behaviours should be considered as variants of the same behaviour rather than distinct sequential phases. Furthermore, none of these behaviours was ever expressed by scent or sighthounds, whose approach was qualitatively very different from that of pointing dogs. Approach by sighthounds was discussed above; scent hounds approach the prey by closely following a scent trail, with more energetic and less inconspicuous movement than pointing dogs' stalking. The absence of anything close to pointing/stalking in both scent and sighthounds raises the question of whether these behaviours were necessarily part of an ancestral sequence. The doubt is further strengthened by considering a phylogenetic standpoint. In fact, wolves are generally not considered stalk hunters, and while stalking can be part of their repertoire of predatory behaviours, it is not always present, at least with the typical larger prey of wolves (Mech et al., 2015).

The dog approach often set the prey off into fleeing, in which case the dog started chasing. However, if the prey did not move when being reached by the dog, the latter could express behaviours such as touching with paws, nose or muzzle, or jumping on the prey with the front legs. Behaviours like those included in teasing are also reported for wolves and other canids. For instance, pouncing is reported in foxes and coyotes, as aimed at securing/immobilising the prey, or

as a substitution of the chase, before biting (Coppinger & Coppinger, 2002; Wells & Bekoff, 1982). However, we did not see biting right after teasing in dogs, suggesting that the behaviour might have a different function in this species. The preys eventually move or flee, engaging the dog in lunge or chase, respectively. This would raise the question whether biting requires a prior chase in the predatory sequence. Alternatively, it is possible that biting was not observed as being inhibited, which is one of the presumptive effects of the selection that originated breed-specific sequences. To this regard, it should be emphasised that we only observed teasing behaviours in pointing dogs. However, as these were the only videos in which the prey did not move, it is impossible to state whether these behaviours are group specific or rather depend on the behaviour of the prey, being potentially expressed by any dog when encountering a motionless prey. The latter idea would be in line with descriptions by Coppinger of 'paw' and 'forefoot stab' which are not restricted to the pointing dogs' group (Coppinger et al., 1987).

The chase was similarly expressed by dogs of different groups, with differences in the extent of the behaviour linked to the nature and motion of the prey – for birds, the chase was much shorter than for mammals – and differences in speed and agility linked to breed-specific characteristics. In general, dogs from any of the three groups started to chase as soon as the prey started fleeing. However, we cannot exclude that dogs started to chase after some trained signal from the hunter, who was often not visible or clearly heard in the videos we used. Low latency between human signals and dog responses, is a crucial measure of efficacy in dog training (China et al., 2020).

Additionally, cooperation with handlers is a fundamental trait sought in pointing dogs, particularly in hunting contexts (Arvelius & Klemetsdal, 2013). It is known that in hunting competition environments dogs are generally expected to avoid chasing prey unless explicitly commanded to do so. For all these reasons, and because of the unknown level of training and hunting experience of the dogs in the analysed videos, we cannot rule out the handler's immediate signal to the movement of the prey, which could have triggered the prey chase response in the dogs. Nevertheless, we would lean more toward the hypothesis that the movement of the prey elicited the chasing phase. In fact,

the triggering effect of the prey movement was consistently observed during the instructional hunt, where we made the *ad hoc* videos, and where the hunters were instructed not to provide training signals to the dog. Moreover, the natural tendency of predators to chase moving prey is well documented (Gancedo et al., 2020; Wilson et al., 2015). This contrasts with the presumptive inhibition of chasing in this group of dogs, proposed by Coppinger and collaborators (Coppinger & Coppinger, 2002), or at least indicates that the behaviour could be largely influenced by learning/training.

Regarding the bite phase, we opted to focus mainly on the first bite landed on the prey. The function of such bite was defined as to catch the prey and land it still or keep it on the ground, corresponding to Coppinger's 'Grab bite'. No clear differences were observed between the breed groups in this behaviour, other than those inevitably related to the nature and behaviour of the prey. Subsequent bites and behaviours expressed by the dogs were more varied, and largely influenced by other factors, including behaviour of the prey, of other dogs and of the hunter/handler. In some instances, we observed other kind of bites, corresponding to what Coppinger describes as killing bite and head-shake bite. We did not observe dissecting bites or prey consumption, most likely because hunting dogs are trained to inhibit this behaviour (Coppinger et al., 1987; Lord et al., 2016).

As regards the stimuli that determined the transition between phases, they were very clear in some instances, namely the movement of the prey initiating the chase and the closeness of the prey eliciting biting attempts or teasing behaviour. Conversely, no visible stimuli were observed that elicited the transition between search and approach. Most likely the onset of the approach is attributable to successful detection of an olfactory trail, but due to the lack of evidence for the presence and intensity of odorants, it is impossible to determine the effectiveness and specificity of the stimuli. Even less clear is what determines the alternation between stalking and pointing during the approach of pointing dogs. Although in this case changes in the intensity of the odour trail could also play a role, other factors cannot be excluded. For example, detection of small movements by prey could induce the dog to stop in a pointing stance. Another possibility is that alternations are

regulated by a time-dependent mechanism, regardless of the duration or characteristics of external stimuli. In this regard, studies in rodents suggest that the timing of immobility bouts after an evoking stimulus is determined by both genetics and learning (Schaap et al., 2013); although clearly expressed in a different context, the duration of point-related immobility, and its alternation with stalking, could be under the control of similar mechanisms in dogs.

The description of the predatory sequence provided in this paper was based on a relatively small number of predatory events. In view of the variety of behaviours expressed by dogs in this context, it certainly cannot be regarded as exhaustive. However, as the ethogram was constructed around functional phases, eventual observations of other behaviours should be easily incorporable into the outlined structure. In this sense, we believe that the present ethogram could represent a necessary and useful starting point for improving knowledge about predatory the behaviour of dogs. There are several questions that would need answers, some of which were raised by observations made during this study. First, there was not always consistency between the behaviours we observed, and predatory sequences previously described in the literature. Although no conclusive considerations can be made from our results, there certainly is a need to better identify the ancestral predatory sequence from which sequences of modern specialised breeds/breed groups have originated. Moreover, while it is quite evident that the behaviours were highly consistent within the same group of dogs and, limited to some phases, very different between the groups, the exact role of the breed on the expression of predatory behaviour remains an open question. Since dogs of specific breeds are used for specific types of hunts, it was impossible to determine whether some behaviours are elicited by the specific prey type rather than breed, or, more generally, the weight of genetic predispositions rather than training on the expression of these behaviours.

REFERENCES

- Akkad, D. A., Gerding, W. M., Gasser, R. B., & Epplen, J. T. (2015). Homozygosity mapping and sequencing identify two genes that might contribute to pointing behavior in hunting dogs. *Canine genet. epidemiol.*, 2(1), 1–13. <https://doi.org/10.1186/S40575-015-0018-5>
- Arhant, C., Winkelmann, R., & Troxler, J. (2021). Chewing behaviour in dogs—A survey-based exploratory study. *Appl. Anim. Behav. Sci.*, 241, 105372. <https://doi.org/10.1016/j.applanim.2021.105372>
- Arvelius, P., & Klemetsdal, G. (2013). How Swedish breeders can substantially increase the genetic gain for the English Setter's hunting traits. *J. Anim. Breed. Genet.*, 130(2), 142–153. <https://doi.org/10.1111/jbg.12026>
- Bateson M., & Martin P. (2021). *Measuring Behaviour: An Introductory Guide*. Cambridge University Press.
- Borchelt, P. L. (1983). Aggressive behavior of dogs kept as companion animals: classification and influence of sex, reproductive status and breed. *Appl. Anim. Ethol.*, 10(1–2), 45–61. [https://doi.org/10.1016/0304-3762\(83\)90111-6](https://doi.org/10.1016/0304-3762(83)90111-6)
- Brockmann J.H. (1994). Ethograms Measuring Behavior: Ethograms, Kinematic Diagrams, and Time Budgets. *Technical Document, Department of Biology, University of Florida, USA. Department of Biology, University of Florida.*
- Chávez, G. A., & Opazo, Á. J. (2012). Predatory aggression in a German shepherd dog. *J. Vet. Behav.*, 7(6), 386–389. <https://doi.org/10.1016/j.jveb.2012.02.004>
- China L, Mills DS & Cooper JJ (2020) Efficacy of Dog Training With and Without Remote Electronic Collars vs. a Focus on Positive Reinforcement. *Front. Vet. Sci.* 7:508. <https://doi.org/10.3389/fvets.2020.00508>
- Christiansen, F. O., Bakken, M., & Braastad, B. O. (2001). Behavioural differences between three breed groups of hunting dogs confronted with domestic sheep. *Appl. Anim. Behav. Sci.*, 72(2), 115–129. [https://doi.org/10.1016/S0168-1591\(00\)00204-0](https://doi.org/10.1016/S0168-1591(00)00204-0)

- Coppinger, R., Glendinning, J., Torop, E., Matthay, C., Sutherland, M., & Smith, C. (1987). Degree of behavioral neoteny differentiates canid polymorphs. *Ethol.*, 75(2), 89-108.
<https://doi.org/10.1111/j.1439-0310.1987.tb00645.x>
- Coppinger, R., & Coppinger, L. (2002). *Dogs: a new understanding of canine origin, behavior and evolution*. University of Chicago Press.
- Creel, S., & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Anim. Behav.*, 50(5), 1325-1339. [https://doi.org/10.1016/0003-3472\(95\)80048-4](https://doi.org/10.1016/0003-3472(95)80048-4)
- D'Ingeo, S., Iarussi, F., De Monte, V., Siniscalchi, M., Minunno, M., & Quaranta, A. (2021). Emotions and Dog Bites: Could Predatory Attacks Be Triggered by Emotional States? *Animals.*, 11(10), 2907. <https://doi.org/10.3390/ANI11102907>
- Estes, R. D., & Goddard, J. (1967). Prey Selection and Hunting Behavior of the African Wild Dog. *J. Wildl. Manag.*, 31(1), 52–70. <https://doi.org/10.2307/3798360>
- Fox, M. W. (1976). Effects of domestication on prey catching and killing in beagles, coyotes and F2 hybrids. *Appl. Anim. Ethol.*, 2(2), 123–140. [https://doi.org/10.1016/0304-3762\(76\)90041-9](https://doi.org/10.1016/0304-3762(76)90041-9)
- Gadbois, S., Sievert, O., Reeve, C., Harrington, F. H., & Fentress, J. C. (2015). Revisiting the concept of behavior patterns in animal behavior with an example from food-caching sequences in Wolves (*Canis lupus*), Coyotes (*Canis latrans*), and Red Foxes (*Vulpes vulpes*). *Behav. Process.*, 110, 3–14.
<https://doi.org/10.1016/J.BEPROC.2014.10.001>
- Gancedo, B., Salido, C., & Tomsic, D. (2020). Visual determinants of prey chasing behavior in a mudflat crab. *J. Exp. Biol.*, 223(6), jeb217299. <https://doi.org/10.1242/jeb.217299>
- Gifford Jr, F. (1959). Statistical properties of a fluctuating plume dispersion model. In *Advances in geophysics* (Vol. 6, pp. 117-137). Elsevier. [https://doi.org/10.1016/S0065-2687\(08\)60099-0](https://doi.org/10.1016/S0065-2687(08)60099-0)
- Grier, J. W. (1984). *Biology of animal behavior* (Times Mirror, Ed.). Mosby College Publishing.
- Henry, J. D. (2013). *Red fox: the catlike canine*. Smithsonian Institution.

- Holling, C. S. (1965). The Functional Response of Predators to Prey Density and its Role in Mimicry and Population Regulation. *The Memoirs of the Entomological Society of Canada*, 97(S45), 5–60. <https://doi.org/10.4039/ENTM9745FV>
- Lehner, P. N. (1976). Coyote Behavior: Implications for Management. *Wildl. Soc. Bull.*, 4(3), 120–126. <https://www.jstor.org/stable/3780989>
- Lenth, B. E., Knight, R. L., & Brennan, M. E. (2008). The Effects of Dogs on Wildlife Communities. *Nat. Areas J.*, 28(3), 218–227. [https://doi.org/10.3375/0885-8608\(2008\)28\[218:TEODOW\]2.0.CO;2](https://doi.org/10.3375/0885-8608(2008)28[218:TEODOW]2.0.CO;2)
- Lloyd, H.G. (1980) *The Red Fox*; Batsford: London, UK.
- Lord, K., Schneider, R. A., & Coppinger, R. (2016). Evolution of working dogs. In *The Domestic Dog: Its Evolution, Behavior and Interactions with People: Second Edition* (pp. 42–66). Cambridge University Press. <https://doi.org/10.1017/9781139161800.004>
- MacArthur, R. H., & Pianka, E. R. (1966). On Optimal Use of a Patchy Environment. *Am. Nat.* 100(916), 603–609. <https://doi.org/10.1086/282454>
- MacNulty, D. R., Mech, L. D., & Smith, D. W. (2007). A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *J. Mammal.*, 88(3), 595–605. <https://doi.org/10.1644/06-MAMM-A-119R1.1/2/JMAMMAL-88-3-595-FIG3.JPEG>
- Manor, R., & Saltz, D. (2004). The impact of free-roaming dogs on gazelle kid/female ratio in a fragmented area. *Biol. Conserv.*, 119(2), 231–236. <https://doi.org/10.1016/J.BIOCON.2003.11.005>
- McDonnell, S. M., & Poulin, A. (2002). Equid play ethogram. *Appl. Anim. Behav. Sci.*, 78(2–4), 263–290. [https://doi.org/10.1016/S0168-1591\(02\)00112-0](https://doi.org/10.1016/S0168-1591(02)00112-0)
- McLennan, T. (2023). Review of literature on interventions aimed at resolving problems caused by predatory behaviour in dogs (*Canis familiaris*). *Appl. Anim. Behav. Sci.*, 106037. <https://doi.org/10.1016/j.applanim.2023.106037>

- McLennan, T., 2023. Does the attention a dog pays to their owner increase after the dog engages in activities that mimic the predatory preferences of that dog (*Canis familiaris*). *Appl. Anim. Behav. Sci.* 263. <https://doi.org/10.1016/j.applanim.2023.105944>
- Mech, L. D., Smith, D. W., & MacNulty, D. R. (2015). *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*. University of Chicago Press. <https://doi.org/doi:10.7208/9780226255286>
- Mehrkam, L. R., Hall, N. J., Haitz, C., & Wynne, C. D. L. (2017). The influence of breed and environmental factors on social and solitary play in dogs (*Canis lupus familiaris*). *Learn. Behav.*, 45(4), 367–377. <https://doi.org/10.3758/s13420-017-0283-0>
- Moehlman, P. D. (1987). Social organization in jackals: the complex social system of jackals allows the successful rearing of very dependent young. *Am. Sci.*, 75(4), 366-375. <https://www.jstor.org/stable/27854716>
- Okada, A., Honma, M., Nomura, S., & Yamada, Y. (2007). Oral behavior from food intake until terminal swallow. *Physiol. Behav.*, 90(1), 172–179. <https://doi.org/10.1016/J.PHYSBEH.2006.09.032>
- Peterson, R. O., & Ciucci, P. (2003). The wolf as a carnivore. In *Wolves: Behaviour, ecology and conservation* (pp. 104–130). University of Chicago Press.
- Ridgway, M. (2021). Hunting Dogs. *Vet. Clin. North Am. Small Anim. Pract.*, 51(4), 877–890. <https://doi.org/10.1016/j.cvsm.2021.04.006>
- Schaap, M. W. H., Van Oostrom, H., Doornenbal, A., Van 't Klooster, J., Baars, A. M., Arndt, S. S., & Hellebrekers, L. J. (2013). Nociception and Conditioned Fear in Rats: Strains Matter. *PLoS One*, 8(12), e83339. <https://doi.org/10.1371/JOURNAL.PONE.0083339>
- Schilder, M. B., van Der Borg, J. A., & Vinke, C. M. (2019). Intraspecific killing in dogs: Predation behavior or aggression? A study of aggressors, victims, possible causes, and motivations. *J. Vet. Behav.*, 34, 52–59. <https://doi.org/10.1016/j.jveb.2019.08.002>

- Schleidt, W. M., Yakalis, G., Donnelly, M., & McGarry, J. (1984). A Proposal for a Standard Ethogram, Exemplified by an Ethogram of the Bluebreasted Quail (*Coturnix chinensis*). *Zeitschrift Für Tierpsychologie*, *64*(3–4), 193–220. <https://doi.org/10.1111/j.1439-0310.1984.tb00360.x>
- Schmutz, S. M., & Schmutz, J. K. (1998). Heritability estimates of behaviors associated with hunting in dogs. *J. Hered.*, *89*(3), 233–237. <https://doi.org/10.1093/JHERED/89.3.233>
- Seremak, B., Wojciechowska, A., Pilarczyk, B., & Tomza-Marciniak, A. (2023). An Ethogram of the Reproductive Behaviour of the American Mink (*Neovison vison*) in Farmed Conditions. *Animals*, *13*(3), 443. <https://doi.org/10.3390/ANI13030443>
- Spagnuolo, O. S. B., Incorvaia, D. C., Johnson, E. T., & Roberts, E. K. (2021). A question of behaviors: How to design, test, and use an ethogram. *Exploring Animal Behavior in Laboratory and Field*, 3–17. <https://doi.org/10.1016/B978-0-12-821410-7.00023-6>
- Strauss, E. (2006). An ethogram developed on captive eastern coyotes *Canis latrans*. *Can. Field-Nat.*. <https://doi.org/10.22621/cfn.v120i3.317>
- Taborsky, M. (1988). Kiwis and dog predation: observations in Waitangi State Forest. *Notornis*, *35*(3), 197–202.
- Udell, M. A., Ewald, M., Dorey, N. R., & Wynne, C. D. (2014). Exploring breed differences in dogs (*Canis familiaris*): Does exaggeration or inhibition of predatory response predict performance on human-guided tasks? *Anim. Behav.*, *89*, 99–105. <https://doi.org/10.1016/j.anbehav.2013.12.012>
- Verrell, P. (1982). The sexual behaviour of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). *Anim. Behav.*, *30*(4), 1224–1236. [https://doi.org/10.1016/S0003-3472\(82\)80215-7](https://doi.org/10.1016/S0003-3472(82)80215-7)
- Wells, M. C., & Bekoff, M. (1982). Predation by Wild Coyotes: Behavioral and Ecological Analyses. *J. Mammal.*, *63*(1), 118–127. <https://doi.org/10.2307/1380678>
- Wilson, R. P., Griffiths, I. W., Mills, M. G., Carbone, C., Wilson, J. W., & Scantlebury, D. M. (2015). Mass enhances speed but diminishes turn capacity in terrestrial pursuit predators. *Elife*, *4*, e06487. <https://doi.org/10.7554/eLife.06487>

Yanes, M., & Suárez, F. (1996). Incidental Nest Predation and Lark Conservation in an Iberian Semiarid Shrubsteppe. *Conserv. Biol.*, *10*(3), 881–887. <https://doi.org/10.1046/J.1523-1739.1996.10030881.X>

Acknowledgments

We are very grateful to Marco Martini, who helped us in collecting valuable video material.

STATEMENTS AND DECLARATION:

Funding: The present study was supported through funds of University of Padua (Post-doc grant number BIRD229302/22 awarded to M.L. and PhD scholarship awarded to C.G.) and of the Italian Ministry of University and Research (PhD scholarship on Green Themes, DM 1061/2021, awarded to A.B.).

Conflicts of interest: The authors declare no conflict of interest.

Ethics approval: This study does not require ethical approval as data were collected from opportunistic recordings where individuals were not framed, or publicly available videos.

Data Availability: This work does not contain datasets.

Author contributions: Conceptualization: P.M, L.M; Data curation: A.B, M.L, C.G; Formal analysis: A.B; Funding acquisition: P.M, L.M; Investigation: A.B, M.L, C.G; Methodology: A.B, P.M, L.M; Supervision: P.M, L.M; Writing - original draft: A.B; Writing - review & editing: P.M, L.M.

Declaration of interests

1. Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author statement

Conceptualization: P.M, L.M; Data curation: A.B, M.L, C.G; Formal analysis: A.B; Funding acquisition: P.M, L.M; Investigation: A.B, M.L, C.G; Methodology: A.B, P.M, L.M; Supervision: P.M, L.M; Writing - original draft: A.B; Writing - review & editing: P.M, L.M.

Highlights:

- 60 videos of dogs expressing different predatory behaviour were analysed
- The functional phases of the predatory sequence: search, approach, chase, bite
- Behaviours in each phase is organized into 3 levels of detail and behavioural focus
- Ethogram shows consistency in the sequence and breed-specific differences in phases