A multidimensional framework for studying social predation strategies

Stephen D. J. Lang*[a,b] and Damien R. Farine*[a,b,c]

[a] Department of Collective Behaviour, Max Planck Institute for Ornithology, Konstanz, Germany

[b] Chair of Biodiversity and Collective Behaviour, Department of Biology, University of Konstanz, Konstanz, Germany

[c] Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, U.K.

ABSTRACT

Social predation—the act of hunting and feeding with others—is one of the most successful life-history traits in the animal kingdom. Though many predators hunt and feed together, a diversity of mechanisms exist by which individuals forage socially. However, a comprehensive framework capturing this diversity is lacking, preventing us from better understanding cooperative forms of predation, and how such behaviours have evolved and been maintained over time. We outline a framework of social predation that describes five key behavioural dimensions: sociality, communication, specialisation, resource sharing, and dependence. By reviewing examples of social predation, we demonstrate the strength of a multidimensional approach, highlighting key commonalities and differences among species, and informative cross-dimensional correlations. These patterns highlight different potential evolutionary pathways and end-points across a multidimensional social predation spectrum.

Keywords: cooperation, foraging, hunting, group living, mutualism, predator-prey.

1. UNDERSTANDING SOCIAL PREDATION

Social predation allows groups of **predators** to find, target and kill larger or more numerous prey with greater efficiency than any individual can manage alone. **Social foraging** (searching for food) and **social** or **group hunting** (pursuing and capturing prey) provide many fitness benefits to individual predators; from enhanced prey detection [1] to the acquisition of additional resources [2-4], and is thought to be a key promoter of the evolution of group living [5, 6]. For example, larger prides of lions (*Panthera leo*) are able to kill larger prey than smaller prides [7, 8]. Social predation is likely to have caused major shifts in the co-evolutionary arms race between predators and their prey [9]. Yet, while social predation has been repeatedly proposed as a classic case of cooperation, the mechanisms underpinning the process of social predation could be relatively simple, without the need for cooperation and instead arising via mutualisms and direct fitness benefits [10].

Despite extensive research on social predation, very little is known about how many times and in how many different forms it has evolved across taxa. Objective research has been restricted by the absence of a framework that quantifies the different forms of social predation. For example, groups containing individuals from more than one species can exhibit social predation behaviours that fit existing descriptions of **cooperation** [11-13] (see **Box 1: Interspecific cases of social predation**), thus highlighting limitations in the current approaches to describing and studying social predation. A robust framework is required to allow the similarities and differences among different groups of social predators to be more clearly evaluated. Such an evaluation would provide clearer insight into the evolutionary pathways that have led to the widespread strategies used by social predators throughout the animal kingdom.

We propose a novel framework to classify social predation among species according to five key dimensions of behaviour. Though the term ‘social predation’ has been previously used to “[cover the] complexities of finding prey and avoiding predation in groups” (and so including foraging behaviour of social herbivores) [14], here we limit it to include the range of different group hunting strategies used by **social predators** (animals that find, capture, and kill mobile prey animals). By extensively reviewing examples of social predation from the literature, and applying the framework to these examples, we demonstrate the strength of a multidimensional perspective. Our approach can identify commonalities in predation strategies across species, and linkages across dimensions. In creating this framework, we encourage experts on each species to report their findings using consistent and precise terminology. Such a framework will enable researchers to draw robust comparisons of different species, facilitate greater focus for future research in a rapidly modernising field (see **Box 2 – How technology is advancing the understanding of animal movement**), and ultimately allow us to better understand the evolution of this diverse set of behaviours.

2. EXISTING FRAMEWORKS OF SOCIAL PREDATION

Existing classification frameworks for social predation constitute one-dimensional continuums [15-17]. Early studies focused their terminology on cooperation, defining it as a single behavioural trait [18-20] (hence the current common usage of 'cooperative hunting'). Boesch & Boesch [15] were the first to outline a framework to delineate the "increasing complexity of organization between hunters". They based their ranked definitions of cooperation on how each individual of a group relates in time and space to its peers: showing similarity, synchrony, coordination, or collaboration (see **Supplementary Table 1**). Later, Ellis *et al.* [16] (**Supplementary Table 2**) and Bailey *et al.* [17] (**Supplementary Table 3**) outlined broader classification frameworks with additional hunting classes (Ellis' illustrated using raptors, Bailey's using Carnivora – though both are more widely applicable). These additions improved the Boesch & Boesch framework by distinguishing the passive 'cooperation' of aggregated predators independently attracted to common resources, from the active cooperation among individuals in hunting groups. Both frameworks added greater consideration for different features of cooperation during hunting (resource sharing, division of labour), and highlighted cases of pseudo-cooperative hunting.

3. A MULTI-DIMENSIONAL PERSPECTIVE

When formalizing social predation using one-dimensional frameworks that range from non-social foraging to cooperative hunting strategies [15, 16], it quickly becomes clear that current frameworks struggle to fully describe the diversity of social predation phenomena found in the animal kingdom (**Box 3: Scoring with existing frameworks**). Take the comparison of two social predator species currently classified as cooperative hunters: the lionfish (*Dendrochirus zebra*, taken from [21]), and the wolf (*Canis lupus*, taken from [22]). Socially, both species have distinct motivations for grouping: lionfish are commonly solitary, and form temporary groups with the main purpose of foraging (though have been observed resting together [23]), whereas wolves live in stable groups that live and hunt together. Their methods of hunt-initiating communication also differ: lionfish flare their fins as an active signal to hunt together, whilst wolves appear to use the behaviour of group **conspecifics** as passive cues to initiate hunting (but see [24]). During hunting, lionfish alternate equally in specialist roles by taking turns at the front (where foraging success is greatest), but wolves appear to hunt using **collective** movement rules [22, 25]. Following a successful hunt, wolves will divide the prey between pack members (according to dominance rank), whereas individual lionfish aim to maximise their own intake. Clearly, each species' strategy contains different elements; each with varying levels of complexity.

We propose using a framework that captures behaviour across multiple dimensions. Our aim is to more accurately capture the range of behaviours associated with social predation, thus facilitating clearer comparisons across taxa, and ultimately the identification of different potential evolutionary pathways to social predation. This framework describes five fundamental dimensions of social predation (see **Figure 1**), and is designed from the perspective of the individual and its interactions with other group members (for a framework linking predator behaviour to prey size and distribution, see [8]). Social predation behaviours for each dimension are divided into subclasses, and ranked according to the increasing level of individual investment into actions that maximize the benefits or success of the group. Below, we define the features of each dimension, and illustrate them using taxonomically broad examples from the literature. Each dimension and sub-section number relates to the framework outlined in Figure 1.

SOCIALITY (Interactions between individuals when foraging and feeding)

ASOCIAL (0) **Solitary**

Animals actively avoid or deter other individuals when foraging or feeding. Examples of this asocial behaviour are common in animals that use discrete territories occupied by a single individual, like tiger (*Panthera tigris*) [26], or pike (*Esox lucius*) [27], or by mated pairs that hunt separately, such as sparrowhawk (*Accipiter nisus*) [28].

ASOCIAL (1) **Aggregations**

Predators forage solitarily but form **aggregations** at common resources. For example, annual salmon runs draw large numbers of brown bears (*Ursus arctos*) to spawning grounds [29]. Although animals in such aggregations appear to form temporary groups, each individual forages independently.

SOCIAL (2) **Group foraging with inconsistent membership**

Individuals gain benefits from group-level **collective foraging**, which is thought to increase per-capita success with group size [30]. Group membership however, is unstable. Such groups are typically composed of unrelated individuals and have rapid membership turnover, exhibiting **fission-fusion** dynamics [31]. Many examples also exist of interspecific groups forming for the purpose of foraging (see Box 1), such as giant moray eels (*Gymnothorax javanicus*) and groupers (*Plectropomus pessuliferus*) that have been observed hunting together [11]. While in some cases the primary driver for forming groups is to reduce predation [6, 14] (typically **mesopredators** such as piranhas or penguins avoiding **superpredators** [32-34]), grouping can also increase hunting success [14]**.**

SOCIAL (3) **Group foraging with consistent membership**

Individuals forage and feed in groups with consistent membership over time. Forming **socially-stable** groups can reduce the level of agonistic interactions and increase predation success among individuals. Groups can consist of unrelated individuals, and generally form in response to some ecological pressure: for instance, improvements in the detection and capture of prey [14], or the cooperative breeding and group caring of young [35]. Individual sperm whales (*Physeter macrocephalus*) for example, have greater foraging success when hunting as groups, but studies suggest their gregariousness is more likely to have evolved through mutual caring of calves [36-38]. Further, many animals that form socially stable groups also have sub-groups of individuals that hunt for the group, which has been observed in several well-studied mammal groups. For instance, male lions, and the females of some chimpanzee (*Pan trogolodytes*) groups rarely participate in hunts [39-42] – though membership is still highly predictable in these hunting groups.

<u>COMMUNICATION</u> (Communication between individuals)

NO SIGNALLING (0) **No response to other individuals**

Individuals do not modify their foraging behaviour in response to the behaviour of others.

NO SIGNALLING (1) **Public/Social Information use**

Group cohesion during foraging or at resources is driven by passive communication between individuals. Social information (using cues generated by others, i.e. **local enhancement**) is a mechanism that can lead to many emergent group-level properties [43, 44], including maintaining **coordination** [45]. Numerous animals choose between feeding sites based on the presence of others, using visual [46-48] or auditory cues [49]. Even in several socially stable species, it appears that individuals rely on simple passive behavioural cues to **synchronise** hunting [22, 39].

SIGNAL (2) **Recruitment/signalling at resources**

Predators use active signals to recruit or synchronise others at discovered food resources. Recruitment of group members can enhance prey capture success and individual foraging efficiency [50], or for mesopredators recruiting larger groups can help reduce individual vigilance for superpredators [51]. The active signalling of food discovery can be via different modalities, but is most frequently communicated using vocalisations [52]. For example, cliff swallows (*Hirundo pyrrhonota*) that find insect swarms use vocal ‘squeak calls’ to signal conspecifics to feed [50]. Communication at discovered prey also appears to function as a means to synchronise prey capture in certain groups of predators, such as packs of dhole (*Cuon alpinus*) [53] and schools of mormyrid fish (*Mormyrops anguilloides*) [54].

SIGNAL (3) **Recruitment/signalling to forage**

Predators use active signalling to initiate foraging (prior to discovering resources). In African wild dogs (*Lycaon pictus*), group members use a ‘rally ceremony’ to encourage other pack members to start a hunt [55] whilst African penguins (*Spheniscus demersus*) employ a ‘head-dipping’ signal to synchronise foraging dives [32]. In fish, groupers make a referential gesture to recruit moray eels [11, 56], whilst lionfish flare their fins to recruit other individuals to their hunting parties [21]. Signals among predators are typically used for recruiting extra group members or to synchronise initiation of the hunt.

SPECIALISATION (Role specialisation of individual during hunting)

NO SPECIALISATION (0) **Individuals forage or hunt without coordination**

Individuals in groups (or aggregations) of predators forage and hunt independently. For example, basks of Nile crocodiles (*Crocodylus niloticus*) near river crossings individually seize passing ungulates [57]. Predators in such groups could have interaction rules that are associated with avoiding collision with others [34, 58]. However, the group's hunting success is not improved by behavioural rules associated directly with foraging or hunting.

NO SPECIALISATION (1) **Individuals coordinate using identical collective rules**

Individuals in foraging or hunting groups use identical patterns of behaviour, forming a collective group structure that benefits hunting success [22, 59, 60]. The **coordination** arising from the collective interaction rules plays a key role in increasing the hunting success of the group [45]. Line-formation is a common group-level strategy used by such collective predators, and can function to herd prey into dense groups and prevent escape [60, 61]. Group hunting by predators has also been shown to facilitate the capture of collective prey by inhibiting collective information transfer within prey groups [62].

SPECIALISATION (2) **Temporary roles**

Animals coordinate with other group members, and some or all individuals take on different roles that function as part of a broader hunting strategy. Individually, these roles are adopted flexibly and can even be switched mid-hunt. For example, Harris' hawks (*Parabuteo unicinctus*) use a hunting strategy with interchangeable 'chaser' and 'blocker' roles that function to flush and capture prey from dense vegetation [63]. Hunting strategies often have only one specialised position that is occupied by a random individual, while the rest of the group occupy a common role. In bottlenose dolphins (*Tursiops truncatus*) hunting schools of fish, group members take turns as lead 'chaser', whilst conspecifics form a barrier to force fleeing fish to the surface [64]. Role specialisation is a critical feature of group-level hunting strategies, distinguishing them from purely collective forms of hunting.

SPECIALISATION (3) **Consistent roles**

Individuals consistently occupy the same specific role between hunts, and roles function as part of a broader group-level strategy. For example, in lions, hunting females regularly occupy the left or right side of a 'winging' hunting tactic [65], whilst individual chimpanzees consistently adopt a role of ‘driver’, ‘blocker’, ‘chaser’ or ‘ambusher’ over multiple hunts [66]. Role consistency should enable individuals to practice and perfect role-specific motor control (the benefits of a consistent attack technique has been shown in sailfish: individuals with stronger side-swipe lateralisation experience higher capture success [67], although this example does not represent role specialisation as part of a group-level hunting strategy). Studies on lions show that an individuals’ body type physiologically matches its role [65], suggesting that consistency also improves development of role-specific muscle groups. Having consistent specialised roles in a family group (as suggested in chimpanzees [66] and some killer whale ecotypes [68]) would also be more effective in facilitating learning by offspring.

<u>RESOURCE SHARING</u> (Sharing of acquired resources among individuals)

COMPETITION (0) **Individuals compete to maximize intake and monopolise resources**
Predators compete to forage, and despotic individuals aim to monopolise resources by excluding all others. Competitive resource division can be seen in numerous territorial species, such as sparrowhawks [28].

COMPETITION (1) **Individuals divide resources among hunters according to effort**
Prey is divided amongst individuals via competition at the resource. Such behaviour is common in predator species that forage on inherently divisible prey, such as sailfish (*Istiophorus platypterus*) [69] and seabirds [70] feeding on fish schools, or bats [49] and swallows [50] feeding on insect swarms.

ALLOCATION (2) **Individuals allocate according to social status (not competing)**
Once the prey is captured, it is allocated to group members according to social rank. For example, when groups of mammalian carnivores including lions, African wild dogs or wolves capture large prey, the resource becomes a feeding patch [17]. Larger, more aggressive or more dominant individuals in the group can control access to the resource, and get preferential access [71]. Unequal resource sharing is common in animal groups governed by dominance hierarchies [72]. Similarly, if certain group members expended additional energy when hunting large prey, they are allocated a larger share of the resulting resource. Examples of this type of resource division can be seen in some chimpanzee populations [66] and human hunter-gatherer cultures [73].

ALLOCATION (3) **Individuals allocate according to need**

Individuals share the prey amongst all group members, allocating the resource in a way that maximizes benefit for all group members. In some cases, groups allocate resources to include individuals that did not participate in the hunt. It has also been suggested that sharing behaviour can occur in animal groups containing adults that are incapacitated as a result of illness or injury, such as pods of killer whales (*Orcinus orca*) [74] and neanderthal tribes (*Homo neanderthalensis*) [75].

DEPENDENCE (Importance of social predation for hunting success of individual)

NO/MINIMAL DEPENDENCE (0) **Pay a cost of foraging or hunting in groups (competition)**

Having more than one predator has a detrimental effect on hunting success. For predators such as tiger [26], sparrowhawk [28], and pike [27] that use an ambush hunting strategy, the greatest success is achieved when hunting solitarily. Additional members increase the chance of groups being detected by prey, thus reducing hunting success.

NO/MINIMAL DEPENDENCE (1) **Neutral or small benefits - don't outweigh other costs**

Having more than one individual has a neutral or negligibly beneficial effect on success rate of the group. This is seen in bears aggregating at salmon runs [29], or piranhas shoaling around prey [34]. Any benefits that are accrued are a by-product of other factors (such as via reduced vigilance for mesopredators), and greater hunting ability is not the driving function of grouping.

HIGH DEPENDENCE (2) **Groups acquire resources that individuals cannot**

Individuals gain greater benefits when hunting as a group. It is often the case that larger groups are more successful than smaller groups in detecting elusive prey [14], controlling collective prey (such as dolphins [61, 64] and whales [76] that corral prey), and bringing down large prey (common in terrestrial carnivores [17]).

HIGH DEPENDENCE (3) **Obligate – group is necessary for both survival and reproduction**

Obligate species that can only hunt with others, and have little to no success hunting alone.

Certain species are dependent on group hunting; in brown-necked ravens (*Corvus rufficollis*) [77], individuals are only successful in catching lizards when hunting with others. In other cases, individuals can hunt smaller species alone, but rely on hunting as a group to kill the prey required to sustain reproduction [78]. In colonial insects like myrmicine ants (*Pheidoiogeton diversus*), individuals cannot survive by hunting solitarily, as prey are too large for a single ant to subdue alone [79].

4. DESCRIBING SOCIAL PREDATION USING A MULTIDIMENSIONAL APPROACH

The aim of the social predation framework is to provide novel insights compared to existing options. To test this, we first identified examples of social predation from the literature by searching Google Scholar with specific keywords (see Supplementary Methods for details). We identified 77 studies of social predation from four main vertebrate taxa that exhibit social predation (mammals, fish, birds and other reptiles). In addition, we selected six representative arthropod studies, and all six interspecific examples we could find (see Dataset 1 and Table 4 in Supplementary Material for complete list). For each study, we scored group behaviour across the five dimensions (Fig. 1) to identify their differences and commonalities in social predation features (see Supplementary Table 1, and Supplementary Materials for methodology). In many species, distinct populations could be scored differently across the five dimensions of the framework. Thus, we demonstrate how the framework can also inform about within-species differences by including multiple scores for killer whales. We calculated the variance in inter-observability by having two independent scorers review 20 species, which resulted in only 5 out of 200 scores of differences between the original (never differing by more than one dimension level).

To illustrate the strength of the proposed framework, we applied a dimension-reduction algorithm (t-Distributed Stochastic Neighbour Embedding – or t-SNE [80]) to our scored data. t-SNE arranges high-dimensional data points according to their similarity across dimensions (**Figure 2**). In our data, the pairwise distance between points reflects the level of similarity in scores across all five dimensions. We then applied a standard Gaussian mixture model clustering algorithm [81] to identify clusters of similar species. While comparative studies would use the actual distances between each pair of species or populations, here we use clustering to provide a visual comparison between the outputs of the new social predation framework and those of existing frameworks (see Box 3).

Clustering of species (Figure 2) highlights the spread of interspecific examples across the diversity of predation strategies, and how different populations of the same species can vary. First, we find that most cases of interspecific social predation occur in the same cluster. These include honeybadger (*Mellivora capensis*) with pale chanting goshawk (*Melierax canorus*), and wedge-tailed shearwaters with skipjack tuna. These largely represent cases where one species benefits as a by-product of the other species' hunting activity. By contrast, other interspecific examples are spread across different clusters. The sharptooth catfish (*Clarius gariepinus*) hunting with blunttooth catfish (*Clarias ngamensis*) is contained in a cluster containing yellowtail and bluefin tuna—both species that can be described as coordinated hunters. Atlantic bottlenose dolphins hunting with spotted dolphins sit in a cluster containing species such as red-bellied piranha and bank swallow (*Riparia riparia*), which can be described as aggregative predators. More broadly, the distribution of interspecific groups across these different clusters suggests that social predation strategies are not all exclusively a result of complex kin-selected processes (see Box 1).

The clusters also highlight that different combinations of strategies can be used by different populations of the same species. The social predation framework reveals that several ecotypes of killer whales are found in separate clusters. Type B orca are clustered with species such as wild dogs and humans, potentially representing the most advanced examples of social hunters. Two other ecotypes (Transient and Resident) are found in the same cluster as Harris' hawks and dholes, which are less-developed social hunters, that show high levels of resource sharing and minimal use of active communication. In this context, the framework will be useful for quantifying how social predation strategies vary across populations adapted for living in different ecological conditions (such as different seasons, habitats, or prey type availability).

Clustering reveals both expected and unexpected results. For example, humans are found alongside orcas, lions, and chimpanzees, but surprisingly, this cluster also contains Aplomado falcons and myrmicine ants. Comparisons within and between clusters could be drawn with other characteristics of each species, such as brain size or lifespan. However, the greatest strength of the framework will be to directly compare the scores within and among species across the different dimensions, and we explore such comparisons in the following two sections. Further, future research combining scores using the framework with phylogenetic information could identify whether certain combinations of predation features represent convergent pathways to complex social predation strategies, and examine the dependency structure linking these behaviours (see Section 6: Dependencies across dimensions).

5. CORRELATIONS BETWEEN DIMENSIONS

Because of the inherent nature of social predation, as rank increases in one dimension it is also likely to increase in others (though not necessarily linearly or equally). We used a correlation analysis to explore in more detail the relationships between dimensions (see Supplementary Figure 1). We only found positive correlations, suggesting that all dimensions captured incremental complexity in similar ways. Further, none of the correlations were close to 1, which would have suggested that the framework needed to be collapsed to a smaller number of dimensions. Here, we discuss the five sets of dimensions with correlations above 0.4.

Sociality + Specialisation (0.52) – Role specialisation is likely to require repeated interactions between the same individuals. However, social predation in mixed-species social predator groups allows role specialisation as a species-level trait [11, 82] reducing the costs of finding individuals with the appropriate specialisation traits.

Sociality + Resource sharing (0.46) – Resource sharing requires individuals to reduce their own intake in lieu of others, such as when food is allocated to non-participants after hunts (e.g. [39, 66]). Such behaviour is most common when stable social groups are formed to increase reproductive success.

Sociality + Dependence (0.56) – Living in stable social groups is likely to have enabled animal groups to improve their hunting ability [5]. We hypothesise that increased pressure from predators could induce responses from prey that include larger body sizes and larger groups. The coevolutionary arms race that ensued could have trapped social predators into high dependence.

Specialisation + Resource sharing (0.4) - Specialisation when hunting large prey requires fair allocation of the resource when a kill succeeds. Thus, resource allocation would be important in role-specialised strategies to ensure a mechanism to provide resources for individuals whose roles do not place them near to captured resources (e.g. flushers).

Dependence + Specialisation (0.43) – Specialisation of roles when hunting in groups can improve the per capita capture of prey. Predators that use specialisation to improve hunting success could become dependent on these as their life histories become reliant on the higher resource balance specialised group hunting provides.

Overall, we find the strongest links between specialisation, resource sharing, and sociality. These links highlight potential traits that could have arisen as by-products of others. Such links raise key questions about the evolutionary origins of social predation (see Outstanding Questions), and the dependencies across the different dimensions.

6. DEPENDENCIES ACROSS DIMENSIONS

It is likely that dimensions of social predation have not evolved independently. Though we find that dimensions largely represent different aspects of behavioural space, it is possible that some behaviours first required others to evolve. Thus, only some evolutionary trajectories among the multitude of possible pathways could be possible (forming a tree-like structure). We explore the nature of such dependencies by searching for consistent differences among dimensions across all species. For each species we subtracted every pair of dimensional scores from one another, and plotted the results in histograms (see Supplementary Figure 2). The resulting graphs highlight that sociality appears to underpin all other traits (i.e. across all species, their sociality score is almost always higher than scores in other dimensions), whereas specialisation seems to be dependent on many of the other traits – notably sociality. It is therefore unlikely that specialisation would evolve prior to sociality.

7. IMPLICATIONS AND OUTLOOK

Our framework provides a multi-dimensional approach that more completely describes all the features of social predation. The framework provides guidelines for comprehensive and objective reporting of social predation by outlining keys areas of information that are needed to fully describe the features of social predator systems. Further, our literature search revealed that many different terms have been used in studies of group hunting. We propose ‘social predation’ as a useful umbrella term to describe this diversity of behaviours, and offer a framework as a starting point to operationalise it. As our ability to study social predators continues to improve, relating findings back to the dimensions from this framework will enable further comparative research. Future studies will be able to quantify social predation strategies of animals across taxa, or even across populations of the same species, thus enhancing our understanding of the evolution of social predation.

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AUTHOR CONTRIBUTIONS

SDJL conceived the original idea and collated all data used in analyses. SDJL and DRF outlined the framework, conducted the statistical analyses, and wrote the manuscript.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

MATERIALS AND CORRESPONDENCE

All correspondence and material requests should be addressed to Stephen Lang (slang@orn.mpg.de) and Damien Farine (dfarine@orn.mpg.de).

FIGURES

Figure 1. Each dimension (grey box) is split into four subclasses, scored from 0-3 (coloured circles). Each of the four sub-classes of a dimension can also be more broadly classified by presence or absence of its key feature (social, signalling, specialisation, allocation, or dependence).

Figure 2. Dimensionality reduction of the scores across all five dimensions for 77 taxonomic examples (see Supplementary Figure 3 for all species names). Each point reflects a specific animal group scored using our social predation framework, and outlined letters refer to which taxonomic group they belong to (see Box 1). The scores for each dimension are depicted by differently coloured sections of the star plot, with the increasing size of each coloured section reflecting higher scores (0-3). The dimensionality-reduction algorithm (t-SNE [80]) positions multi-dimensional data points that are more similar closer to one another. The coloured background polygons are the result of a Gaussian Mixture Model clustering algorithm [81] that is used to identify groups of species with similar social predation strategies, enabling comparison to existing frameworks (see Box 3).

REVIEW BOXES

BOX 1 – Interspecific cases of social predation:

Consideration of social predation often comes with a tacit assumption that it requires complex social mechanisms to evolve. However, there are many examples where individuals from different species exhibit social predation behaviours. These suggest that the underlying processes facilitating social predation can be relatively simple. Here we briefly review three examples of interspecific social predation.

Commensalistic relationships can form between predator species when associations benefit individuals from one species at no cost or benefit to **heterospecifics**. Ethiopian wolves (*Canis simensis*), for example, associate with herds of gelada monkeys to form interspecific groups. Gelada herds flush small rodents as they move through vegetation, and Ethiopian wolves have a higher rate of prey capture when moving with baboon troops [83]. The wolves' strategy appears valuable enough that they will forgo the chance to easily take juvenile geladas (resulting in expulsion) so that they can retain the benefits of hunting within the group.

Interspecific groups can also mutualistically benefit all individuals involved. Several studies investigating the associations between seabirds and subsurface predators have shown a higher rate of prey capture for all individuals involved in heterospecific social predation, as each predator species drives prey towards the other [70]. Examples include wedge-tailed shearwaters (*Puffinus pacificus*) and skipjack tuna (*Katsuwonus pelamis*) that non-randomly associate with surface-hunting fish [12]. Though generally facultative (shearwaters can also feed without heterospecifics), there are cases of apparently obligate relationships. Frigate birds (*Fregata spp.*) and sooty tern (*Sterna fuscata*) are rarely seen foraging independently of subsurface predators such as tuna [82].

Sophisticated interspecific relationships also exist where individuals use active communication and have complementary hunting skills that maximize their hunting success when hunting as heterospecific groups. One example is social predation by grouper and giant moray eel [11]. Using body movements, groupers actively signal to morays to initiate foraging, and direct them to the locations of prey. The specific hunting strategies of each species are complementary, with morays flushing prey from crevasses and groupers flushing them into crevasses. The result is that hunting success for both groupers and moray eels is almost five times greater when hunting together than when individuals hunt alone [11]. Such examples demonstrate that certain features of social predation can be found in a range of heterospecific predator groups [84, 85], highlighting the extent to which social predation behaviours can evolve from direct fitness benefits without requiring indirect benefits such as kin selection [35].

***BOX 2* – How technology is advancing the understanding of animal movement**

Modern improvements to animal tracking technologies are enabling researchers to collect fine-scale movement data over extended time periods [86]. Of particular relevance to the study of social predation is the ability to simultaneously track multiple individuals at once. With high-resolution positioning data collected from GPS tags, orientation data using magnometers, and movement data collected using accelerometers, it is now possible to explore in detail some of the mechanisms that underpin the group-level movement dynamics during group hunts.

Recent work investigating social decision-making in baboon troops used modern GPS-collars that collected high-accuracy (0.5m) spatial data at high temporal resolution (1hz), allowing for comprehensive study of individual movements, and analysis of group-level collective outcomes [87]. Such tracking techniques can be effectively applied to social predator systems to study how group members initiate and coordinate hunts, and capture information about the amount of energy hunters expend under different conditions. For example, recent tracking studies on African wild dogs have used high-resolution GPS tags on all members of a pack to investigate the use of group-level hunting strategies in dense habitats [88]. GPS tags with additional functions could also be used to understand aspects of hunting behaviour not possible with conventional tags. For instance, gaps in the understanding of how vocal communication influences hunting behaviour (see **Box 4: Outstanding questions**) could be addressed using GPS tags capable of audio-recording individual vocalisations. More generally, even though studies employing novel technology will rely heavily on theory because of the challenges of carrying field experiments [8, 87, 89], the ability to conduct experiments will also be facilitated by technological advances (e.g. [90]).

One caveat of fitting GPS tags to predators is that the identity, behaviour and fate of prey is often unknown. Future studies will be able to follow whole social groups of both predators and prey simultaneously. This will allow researchers to better understand many aspects of the hunt – from how predators select and pursue targets, the ultimate outcome of predation events, and the downstream responses of prey to predation pressure. Previous research has already demonstrated how combining tracking data from predators and prey can provide novel insights into how predator-prey dynamics shape ecosystem structure [89]. Non-invasive forms of animal tracking that can locate and identify untagged individuals (for example drones) are also likely to become reliable, cost-effective and practical methods to track groups of free-living animals [91-93]. In many cases, these technologies will not replace human observations, but will facilitate better quantification of behaviour during hunts [94, 95].

Finally, combining long-term tracking of animals with modern methods for extracting data on the hormonal profiles from passive samples (e.g. faecal) will yield greater insights into some of the physiological mechanisms underlying group hunting behaviour, as well as prey responses. For example, integrating such data with information from GPS tags about individual propensity to join hunts, their role in the hunt (for example the effort expended or relative position), and the rate of agonistic or affiliative behaviours towards others. Thus, recent technological developments in animal tracking are making it possible to collect more information from a growing selection of social predators and their prey—and for longer periods of time, thus gaining insights into both the proximate and ultimate drivers of social predation.

Figure B2.1. Technology is facilitating new insights into social predation. GPS tags fitted to predators, such as (a) African wild dogs (photo: J. Myatt [88]), and prey, such as (b) plains zebra (photo: D. Rubenstein), will enable detailed studies into the mechanisms of the hunt. (c) Unmanned aerial vehicles (UAVs) will enable simultaneous video tracking of predators and prey (photo: NOAA fisheries, Vancouver Aquarium [93]), while other sensing technologies, such as (d) sonar (image: N.O. Handegard [62]), can be used to track the interactions between predator and prey in more visually-restricted tracking environments.

BOX 3 – Scoring with existing frameworks

All currently used classification schemes of social predation represent one-dimensional continuums, ranging from passive or non-cooperative systems, to fully cooperative groups [15-17]. To evaluate the benefits of using a multi-dimensional approach to quantifying social predation strategies, we identified clusters of species with similar combinations of behaviours in the framework (coloured clusters in Figure 2). We then scored examples using two existing one-dimensional schemes for defining cooperative hunting: Ellis [16] and Bailey et al. [17] (see Supplementary Tables 1-2 for the detailed classification schemes) . Combining these scores enabled us to evaluate the differences between our multi-dimensional framework and current methods of classifying social predation. If the social predation framework makes no improvements on the existing classification methods, we would expect each of the clusters from Figure 2 to align with the classification groups from the existing frameworks.

As shown by Figure **B3.1**, both the Ellis [16] and Bailey [17] frameworks appear to capture only the extremes of the social predation spectrum (which corresponds with our findings from section 7). These extremes are likely to represent what would normally be defined as cooperative social predators (red and green), such as killer whales or chimpanzees; and largely non-social predators (light blue and turquoise) like osprey or crocodiles. By contrast, other species that are clearly clustered in the social predation framework are poorly represented in the existing frameworks, for instance the light green, purple, and pink clusters. The extensive overlap of such clusters, particularly following Bailey's [17] definitions, highlights how using a one-dimensional scheme only partially describes the diversity of hunting strategies exhibited by some social predators.

Figure B3.1. Results of scoring each animal group according to the Bailey [17] (**a**) and Ellis [16] (**b**) frameworks. Each row depicts a specific animal group. The column position of each point denotes the category in which the example fits according to the focal classification scheme. Point colour corresponds to the cluster assigned by the clustering algorithm used in Figure 2, and the intensity of the background colour highlights the relative proportion of animal groups from the same cluster in a single category.

BOX 4 – OUTSTANDING QUESTIONS

Examining the distribution of species scored using our framework has enabled us to identify both gaps in the literature and key questions arising in the study of social predation.

Gaps:

Many studies of social predation only acknowledge the use of communication signals when these are obvious, and the response to cues remains largely untested. As a result, the extent to which groups of predators use active signals or pick up on the cues of others is not completely understood. Wolves, for example, use vocalisations, body posture and olfactory signals to communicate within and between groups [24, 96], but the extent to which they use such signals in the context of hunting – specifically to initiate hunts or synchronise attacks – remains poorly understood. In mixed-species predator groups, it is unclear how much active communication occurs between species, and whether individuals actively target communication to heterospecifics.

Population-level differences appear to be an important source of variation in strategies among groups of social predators. Recent studies support the idea that cultural evolution could play an important population-level role in the formation and maintenance of social predation strategies [97]. Further, very little is known about how such social predation strategies are improved or adapted over time – both on an individual level and between generations [98]. The underlying genetic and developmental mechanisms, as well as plasticity, associated with social predation strategies remain unexplored.

Key questions arising:

The strong clustering emerging from our multi-dimensional framework raises the question of how many different pathways exist for social predation to evolve. Several examples from very different taxonomic groups demonstrate similar social predation strategies, whereas closely related species can demonstrate widely divergent strategies (**Figure 2**). Thus, integrating data using the framework into a phylogenetic analysis will yield novel insights into social evolution, including whether there is any convergent evolution towards social predation strategies.

The strong correlation between sociality and multiple dimensions of the framework raises the question of which traits evolved in response to selection and whether some traits arose as by-products. Which evolved first: the evolution of sociality that enabled predators to capture and share large prey items, or the ability to capture large prey as groups that provided the foundations for sociality? A notable area of research will be to study how social predation fits into predator-prey coevolution, and to determine whether coevolution has trapped social predators into high dependence.

GLOSSARY

Aggregation - Gathering of individuals attracted to a common resource.

Collective - Groups with behaviours that arise from common inter-individual interaction rules.

- **Coordinated (collective)** - Individuals relate in *time and space* to actions of others.
- **Synchronised (collective)** - Individuals relate in *time* to actions of others.

Conspecifics - individuals of the same species.

Cooperative - Working with others (not always as equals).

Fission-fusion - Groups that change in individual membership over time.

Feeding – Consumption of a food resource.

Foraging – The act of searching for a food resource.

Group – Two or more individuals that respond to the behaviour of each other.

Hunting - Active searching, pursuit and capture of mobile prey animals.

Heterospecifics – Individuals of a different species.

Local enhancement - Attraction of an individual by the presence of others.

Mesopredator - A predator that is also preyed on by a superpredator.

Predator - An animal that derives (at least some of) its energy by consuming other mobile animals.

Social foraging - Searching for food (plants/animals) with others.

Social predation - Finding, capturing and consuming other animals with others.

Social predator – A predator that finds, capture and consume animals with others.

Socially-stable - Groups with social ties that persist in time and across contexts (feeding, breeding).

Superpredator - A predator than preys on mesopredators and/or other superpredators.

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