Mobbing in animals: a thorough review and proposed future directions

Nora V Carlson 1

Michael Griesser 2-4

1) Graduate School of Science, Faculty of Science, Kyoto University, Kyoto, Japan

2) Department of Biology, University of Konstanz, Konstanz, Germany

3) Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Konstanz, Germany

4) Center for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany.

Abstract

Mobbing is an important anti-predator behavior where prey harass and attack a predator to lower the immediate and long-term risk posed by it, warn others, and communicate about the predator's threat. While this behavior has been of interest to humans since antiquity, and aspects of mobbing have been well researched for the past 50 years, we still know little about its ecology and the evolutionary pressures that gave rise to this widespread anti-predator behavior. In this review, we explore what mobbing is, how it is used, what its functions are thought to be, and its use as a proxy for cognition, before providing suggestions for specific future avenues of research to improve our understanding of the ecology and evolution of mobbing.

1. INTRODUCTION

Mobbing, a behavior where prey approach, harass and sometimes attack a predator, is a prevalent anti-predator behavior observed across many animal taxa. While mobbing appears to be a vital anti-predator strategy for many species, the behavior itself, as well as its evolution and ecology remain poorly understood. In this review, we explain what mobbing entails and detail its natural history. From there, we move on to discuss how mobbing is quantified and what this means for comparative studies. Then, we outline the main hypotheses regarding the functions of mobbing, how these functions relate to one another and how its primary functions facilitate the evolution of secondary and tertiary functions. We discuss how different motivations can result in similar behavioral outcomes. Finally, to make the findings of different studies more comparable, we call for a standardization of mobbing definition, present a template to allow for better quantification across studies, and suggest overlooked areas of study in mobbing.

1.1 What do we know about mobbing? An overview

1.1.1 What is mobbing?

Mobbing behavior, defined as when one or more prey approach and harass a predator (see below for a comprehensive definition of mobbing), has been of interest to scientists and the general public for a long time. References to mobbing show up in illustrations on Greek pots depicting bird-catchers using mobbing to attract songbirds to a tree covered in a sticky residue for easy capture (Morris, 2009), p. 167 for image) and in Aristotle's writings on nature (Aristotle, 350AD). An early mention of mobbing behavior in the scientific literature is by Grinnell (1920, p.85): "I am aware that Ruby-crowned Kinglets do occasionally assemble to a limited extent in winter; for example, when "mobbing" an owl" (Grinnell, 1920), p.85). Since Grinnell's observation on mobbing in birds, this behavior has been studied widely across different areas of behavioral and ecological research. However, much of this research has largely ignored the general ecology of this behavior, but rather uses mobbing to investigate aspects of communication, learning, and cognition (Table 1). Additionally, although mobbing is widely prevalent across taxa, the focus of mobbing research tends to be on the vocal aspects of mobbing, leaving the non-vocal aspects including body postures and movements largely unstudied (e.g., Altmann, 1956; Curio, 1975; Gottfried, 1979; Ishihara, 1987; Owings & Owings, 1979).

Table 1 A breakdown of mobbing research literature providing details on a) the taxa represented, b) contains a definition of mobbing (yes/no), c) contains a detailed description of mobbing behavior in the studied species, d) the focus of the paper: vocal communication (e.g., syntax, information encoding), cognition (e.g., predator recognition, learning), or mobbing behavior, and e) the type of paper (experimental, observational/descriptive). Table based on N = 337 papers. See Supplementary Table 1 for breakdown of table by paper.

	Paper contents	**Number of papers**
a)	Taxa studied	
	Birds	245
	Mammals	62
	Fish	15
	Invertebrates	5
	Reptiles	3
b)	Paper provides a definition of mobbing	
	Yes	118
	No	218
c)	Paper provides a detailed description of mobbing	
	Yes	97
	No	239
d)	Paper focus	
	Communication	58
	Cognition	52
	Mobbing	161
	Descriptive	49
e)	Paper type	
	Experimental	271
	Descriptive	49
	Review/theoretical	17

1.2 How to define and describe mobbing?

1.2.1 Mobbing behavior

Most researchers who study mobbing can easily differentiate it from other behaviors. The definitions used in the literature, however, vary from the rudimentary, for example "when a prey moves toward and harasses a predator" (Dutour & Randler, 2021, p. 1) to the more specific, such as: "prey animals approaching, gathering around, intently observing and harassing a predator. This harassment encompasses a suite of behaviors that may include vocalizations specific to the mobbing context (i.e., distinct from general alarm/warning calls) and advances towards the predator to inspect, follow, harangue or attack." (Crofoot, 2012, p. 254). A commonly cited definition of mobbing comes from Curio who described it in birds as "birds of one or more species assemble around a stationary or moving predator (potentially dangerous animal), change locations frequently, perform (mostly) stereotyped wing and/or tail movements and emit loud calls usually with a broad frequency spectrum and transients" (Curio, 1978, p. 176)". As with much of the research on mobbing behavior, most of these definitions concern birds and mammals and therefore usually incorporate some aspect of vocal behavior.

In general, the primary function of mobbing is thought to be to remove predators and/or warn others about the presence of predators. Regardless of how mobbing is described, (Bakker & Langermans, 2018; Brudzynski, 2018; Wilson & Hare, 2006) it is a suite of behaviors, including stereotyped movements or postures, fixating on and approaching the predator closely, often moving towards and away from the predator in rapid bursts, aggression towards the predator, and in the case of vocal species, producing specific vocalizations. Across species, mobbing can vary from passive mobbing behavior such as observing and calling from a distance (e.g., in giant otter, *Pteronura brasiliensis,* Leuchtenberger, Almeida, Andriolo, & Cranshaw, 2016*;* or dunnocks, *Prunella modularis,* NC pers obs.) to active, aggressive mobbing behavior and physical contact with a predator (e.g., in red-winged starlings, *Onychognathus moriom* Curio & Regelmann, 1985; or black bass, *Micropterus sp.,* Dominey, 1983; Figure 1). Mobbing can become highly aggressive with some, but not all, species physically attacking the predator, including diving at (birds, Clode, Birks, & Macdonald, 2000), hitting (primates, Boinski, 1988), biting (fish, Hein, 1996a), or stinging (invertebrates, Seeley, Seeley, & Akrathanaku, 1982). While some specific stereotyped behaviors are unique to certain taxa, in birds at least, there are a few commonalities such as tail flicking, wing flicking, bobbing, and raising the crest (Carlson, Healy, & Templeton, 2019; Curio, 1975; Francis, Hailman, & Woolfenden, 1989). Many of

these behaviors are thought to arise proximately from the conflicting desire to both approach and flee the predator (Hinde, 1954a). In other taxa, other types of behavior are commonly found, such as raising the tail and/or hair of the body (mammals, Owings & Coss, 1977), lateral displays (fish, Donaldson, 1984), or biting/stinging (invertebrates, Kastberger, Weihmann, Zierler, & Hötzl, 2014).

Although mobbing is a prominent behavior in many species, descriptions of the stereotyped movements that individuals exhibit during mobbing are often lacking. Only 35.1% of studies that focus on mobbing define mobbing, and 28.9% of studies explicitly describe what mobbing in their study species looks like (Table 1), often simply mentioning that a species mobs, or in many cases, produces mobbing calls. Additionally, there is no consistent labelling used across all taxa. For example, while this behavior is described as mobbing in birds and mammals, many fish and invertebrates display mobbing behavior but here, it is either categorized as predator inspection (e.g., in fish) or labelled something different (e.g., swarming in bees). This lack of clear, detailed information and uniform labelling limits the reader's ability to assess what the author considers mobbing behavior and how species exhibit mobbing behavior. This, in turn, makes recognizing mobbing behavior and comparative work across species difficult. Thus, it is critical to provide a comprehensive and standardized description of mobbing behavior, even in studies that do not entirely focus on mobbing, so that readers understand how mobbing behavior varies across species (Figure 1), and how it compares to mobbing in other species or taxa.

Sense predator cues	Predator inspection	Initiate Mobbing		Attack predator
Functions/behavior	Approach to gather information	Recognize predator	Passive mobbing	Aggressive mobbing
Distance	Far	Intermediate (outside predator strike distance)	Close (within predator strike distance)	Contact
Anti-predator vocalizations	No calls	Few		Many
Distress behaviors and visual signals	None/few (orienting towards predator)	Few (stereotyped and stress behaviors)		Many (stereotyped and aggressive behaviors)
Aggressive behaviors	None	Bluff attacks		Attack

Figure 1 The progression of behavior from detecting a predator, to predator inspection, recognizing a predator, and mobbing including aggressive attacks. Mobbing behavior encompasses a suite of behaviors, including close physical distance, uttering many anti-predator vocalizations (only in vocal species), displaying diverse behaviors and visual signals, and aggression directed towards the predator.

Finally, although mobbing occurs in birds, mammals, fish, invertebrates, and reptiles (Table 1), it is most easily studied in birds due to their conspicuous mobbing behavior. Thus, 74.2% of papers focused on mobbing using birds as a study system followed by studies on mammals (18.8%), fish (4.5%), invertebrates (1.5%), and reptiles (0.9%; Table 1). This taxonomic bias is likely a key reason why emitting "loud calls" is considered a diagnostic mobbing behavior in many of the definitions. However, not all taxonomic groups are equally likely to give loud calls (e.g., invertebrates are less likely to give loud calls than are birds), while others can produce calls outside the perception range of humans (e.g., rodents, bats, fish, Bakker & Langermans, 2018; Brudzynski, 2018; Wilson & Hare, 2006).

1.2.2 What is not mobbing?

Although mobbing is often easily recognized, quantifying it can be difficult. Describing what is not categorized as mobbing, can help clarify where the difference between mobbing and other anti-predator and aggressive behaviors lie. Several behaviors share some similarities with mobbing, but they have very different drivers, costs, and benefits. Predator inspection behavior is one of the most difficult to clearly separate from mobbing as it involves many of the same predator approach and stereotyped behaviors as mobbing (Figure 1). Moreover, predator inspection can reduce the probability of a predator to attack. However, unlike mobbing, predator inspection never includes harassment of the predator or physical contact with the predator, and while predator inspection can escalate into mobbing, the latter cannot deescalate into predator inspection (Figure 1).

Distress calls, flee/freeze calls, and alert calls are anti-predator vocalizations used when encountering predators (Griesser, 2008; Magrath, Haff, & Igic, 2020; Marler, 1955, 1957, 1967), and are sometimes incorporated into mobbing calls. However, when produced alone and in non-mobbing contexts, these calls result in very different responses by others that differ from those associated with mobbing. Distress calls are produced when an individual is already caught by a predator and are thought to serve primarily to startle the

predator into letting the prey go. However, these calls may also serve to attract attention to the predator or situation, resulting in a mobbing event (Branch & Freeberg, 2012). Flee/freeze calls (e.g., passerine zeet calls) are produced when an individual sees an imminent threat and, when heard, results in fleeing and/or freezing behavior respectively to avoid being caught by the predator (Griesser, 2008; Magrath et al., 2020; Marler, 1955, 1957, 1967). While these calls can sometimes be incorporated into mobbing calls, when produced alone, they do not induce mobbing behavior but elicit different, non-mobbing anti-predator behavior.

Finally, aggressive behavior can also occur between conspecifics and other non-predatory heterospecifics, for example when breeding individuals harass and attack others to drive them away (e.g., noisy miners, *Manorina melanocephala,* Arnold, 2000; Dow, 1977). Although many of these behaviors may look like mobbing, the mobber is not threatened and the motivations for removing the intruder are different.
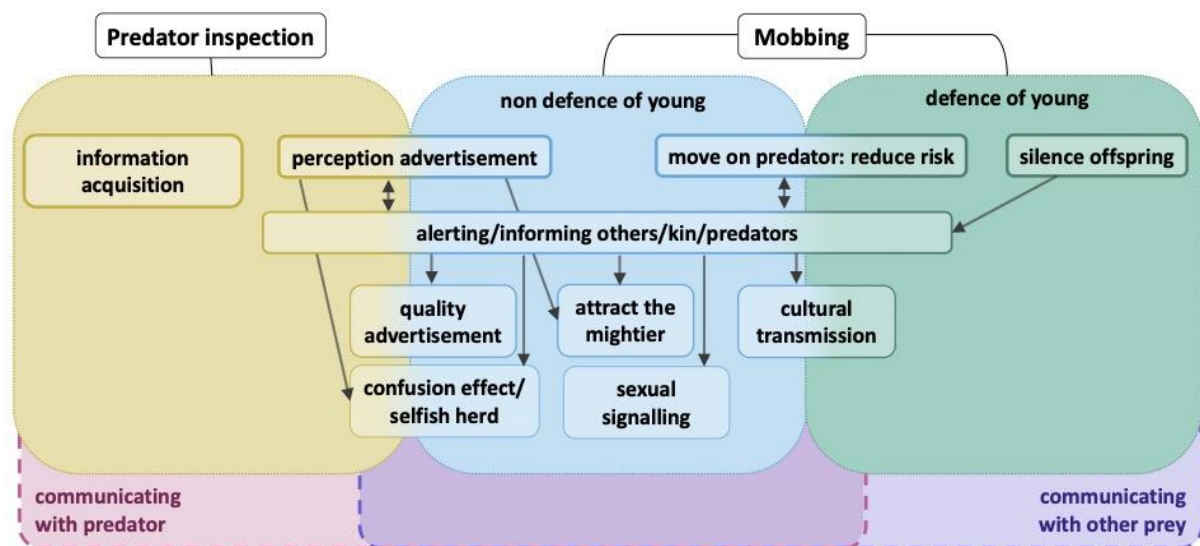
Figure 2 Links between predator inspection (left) and mobbing in non-defense of young (middle) and defense of young contexts (right), and the different functions of these behaviors. Primary functions are in the 1] top level, followed by 2] secondary, 3] tertiary, and 4] quaternary functions in descending order. The boxes on the bottom outlined in dashed lines show the intended receivers of the mobbing signal: the predator (left) or other prey (right) with both predators and other prey as the intended receivers.

1.3 How dangerous is mobbing?

Approaching and mobbing a predator appears quite dangerous, however, quantitative data are lacking. It remains largely unknown how often mobbing happens, how it actually affects the overall predation pressure, or how often birds are injured or even killed during mobbing events. Clearly, mobbing does come with a number of potential direct and indirect costs. The most obvious costs of mobbing a predator are injury or death, either from colliding with other mobbing individuals or the predator (thought to occur very rare, (Conover, 1987), or by being attacked by the predator being mobbed (Curio & Regelmann, 1985). There are many anecdotes describing mobbing events where mobbing individuals were injured or killed (buffy-tufted ear marmoset, *Callithrix aurita,* Corrêa & Coutinho, 1997); capuchins, *Cebus capucinus,* Tórrez, Robles, González, & Crofoot, 2012); American crows, *Corvus brachyrhynchos,* Crofoot, 2012; Denson, 1979); Southern Lapwings, *Vanellus chilensis,* Myers, 1978); several bird species, Sordahl, 1990); several primate species, Crofoot, 2012), but ~~one of the~~ few studies have quantified mobbing in the wild with live predators. For example, during a long-term study of Siberian jays, *Perisoreus infaustus*, five mobbing events were observed during 2,300 field days, and no individual was killed during these events, but hawks and owls account for 95% of deaths of adults (Curio & Regelmann, 1986; Griesser et al., 2017). Also, there is little evidence regarding the cost of a mobber drawing attention to itself with conspicuous signals (Krams, 2001) and therefore possibly increasing the chance of being singled out for an attack.

In addition to direct costs discussed above, there are as yet unexplored indirect costs to mobbing, including (1) the energetic costs (as this behavior is often quite vigorous in nature with increased movement and calling; (Crofoot, 2012); (2) attracting other predators, (e.g., nest predators ((Krams, Krama, Igaune, & Mänd, 2007), or predators of adults (Fang, Hsu, Lin, & Yen, 2020; Smith, 1968), and (3) lost opportunity costs, as mobbing prevents the expression of other behaviors (e.g., foraging or singing to attract a mate (Caro, 2005; Cresswell, 2008; Crofoot, 2012).

1.4 The ontogeny of mobbing

Mobbing behavior can either be innate or learned. Similar to other anti-predator behaviors, both modes of acquisition have been observed even for different predators within the same species. Responses to predators and to the mobbing behavior of others can also differ. These differences likely reflect whether young can observe or learn about the danger a predator poses without being attacked by that predator.

In many species, the response to mobbing calls appears to be innate (especially when young), though these responses are not mobbing responses. For example, Japanese tit *Parus minor* nestlings will rapidly escape from the nest cavity when they hear a snake-specific referential mobbing call that warns nestlings of a snake invading the nest cavity (Suzuki, 2011). After juveniles leave the safety of their home (den, burrow, nest, etc.) and can engage in mobbing behavior themselves, the degree to which mobbing behavior may be learned varies between species. In some species, naïve juveniles engage in mobbing behavior irrespective of the presence of more experienced individuals (e.g., California ground squirrels, *Spermophilus beecheyi*, black-tailed prairie dogs, *Cynomys ludovicianus*, Owings & Coss, 1977; Owings & Owings, 1979), while in others, juveniles do not engage in mobbing, at least early on, but rather observe others mobbing (blue tits, Carlson et al., 2019; American robins, *Turdus migratorius,* Shedd, 1982; black billed magpies, *Pica hudsonia,* Buitron, 1983; Florida scrub jays, *Aphelocoma coerulescens,* Francis et al., 1989; black-tailed prairie dogs*,* Loughry, 1987), or start mobbing only after they observe adults to do so (Siberian jays, Griesser & Suzuki, 2016). This variation may reflect higher costs of mobbing for juveniles than for older individuals as juveniles are physically less capable and coordinated than adults. Alternatively, naïve juveniles may first have to learn to recognize predators as such (Carlson, Healy, & Templeton, 2017a; Griesser & Suzuki, 2016, 2017), or how to mob them safely (Carlson et al., 2019). While the ontogeny of mobbing can provide important evidence for the evolution of mobbing, this aspect remains understudied (but see: Hinde, 1954a, 1954b, 1961). Studying the ontogeny of mobbing would show how commonly this is a learned or innate behavior and which specific aspects of mobbing are learned, e.g., if the associations between predator threat and mobbing are learned, if mobbing calls are learned, and in species where learning plays a role, if learning is limited to a sensitive period early on in life or if it can also occur in adults.

1.5 Who are the recipients of mobbing calls?

Depending on the primary driver of mobbing, mobbing calls are aimed at conspecifics, the predator, and/or other predators. In birds, mobbing calls are thought to be designed as long-distance calls which travel effectively through their habitats (Billings, 2018), and consequently, con- and heterospecifics can eavesdrop on these calls. Eavesdropping is widely prevalent in communities with mobbing species, both within and between taxonomic lineages (e.g., passerine birds, Goodale & Kotagama, 2005; Goodale & Ruxton, 2010; Gunn, Desrochers, Villard, Bourque, & Ibarzabal, 2000; Magrath, Haff,

Fallow, & Radford, 2014; Suzuki, 2016; group living mammals, Crofoot, 2012; Gursky & Nekaris, 2007; birds and mammals, Rainey, Zuberbühler, & Slater, 2004). Even non-vocal species such as lizards (white-bellied copper-striped skink, *Emoia cyanura*; Galapagos marine iguana, *Amblyrhynchus cristatus,* Fuong, Keeley, Bulut, & Blumstein, 2014; Vitousek, Adelman, Gregory, & Clair, 2007) will eavesdrop on mobbing calls and subsequently increase their own anti-predator behavior such as bloating (skinks) or vigilance (iguanas). This prevalence of heterospecific eavesdropping is thought to create large anti-predator communication networks (Magrath et al., 2014) with specific individuals ranging in 'importance' as sources of anti-predator information (Goodale & Ruxton, 2010; Magrath et al., 2014; Templeton & Carlson, 2019). While mobbing behavior in its capacity as an anti-predator behavior has been observed and reported on extensively throughout the years, many aspects of the behavior remain understudied. We still know little about how eavesdropping networks may shape community structure and heterospecific relationships, how the information in mobbing calls travels through the prey community during a predator encounter, and how the presence of aggressive mobbers alters long-term predator movement and predator-prey relationships.

2. QUANTIFICATION OF MOBBING AND USE IN RESEARCH

For most researchers identifying mobbing behavior is easy, but it is difficult but quantifying it, probably because mobbing is so variable within and between taxa. While many studies provide descriptions of mobbing in their species (28.9%; Table 1), many more do not, or use only one specific behavior (often mobbing calls themselves) as a proxy for mobbing behavior (71.1%; Table 1). This lack of specificity creates ambiguity in defining, classifying, and measuring mobbing across experiments and taxonomic groups, making drawing more general conclusions about mobbing difficult, and comparative research all but impossible.

2.1 How is mobbing measured?

Mobbing is often quantified as either a binary category (mobbing vs. not mobbing) or in degrees of intensity (e.g., approaching, approaching and calling, diving; Blancher & Robertson, 1982; Grim, 2007; Marzluff, DeLap, & Haycock, 2015; Owings, Coss, Mckernon, Rowe, & Arrowood, 2001; Table 1). Currently, mobbing (occurrence or intensity) is

measured in six main ways in the literature, each with its own benefits and drawbacks. We describe each of them below.

Table 2 Table showing the six main ways mobbing behavior is measured in the literature.

Measurement	Description	Benefit	Drawback
Calling behavior	The calls individuals produce during mobbing	Obvious and easily quantifiable, very common in birds	Unsuitable measurement for species that only rarely or never produce calls, or the calls lay outside the human perception range (e.g., fish, mammals, invertebrates, reptiles)
Minimum distance to predator	The closest distance an individual approaches to the predator when mobbing	This measurement can easily differentiate between mobbing and predator inspection; in many species individuals do not get as close during predator inspection as during mobbing	This measurement can be influenced by non-predatory factors, e.g., local cover, presence of heterospecifics, season, personal experience
Physical contact/attacks	Individual makes physical contact with predator, or directly attacks it	This behavior is diagnostic of mobbing	This behavior may vary widely in its use across species; many species do not directly physically attack a predator
Level of activity	The overall activity (e.g., calling, approach rate, number of individuals participating) an individual or group is exhibiting	Increases in mobbing activity are a robust measure of degree of danger	This measure can be vague and difficult to quantify and keep consistent across species or studies
Latency to response	The amount of time it takes for an individual to respond to a signal	Useful to study perception and degree of investment or urgency of a signal	It can be difficult to determine if an individual that did not respond did not perceive the signal pertinent or if it did not receive the signal, making negative responses uninformative
Categorical scale	A series of categories defining classes of mobbing response that increase in intensity	Increasingly intense categories allow researchers to tailor responses specifically to the species being studied and the specific mobbing behaviors they exhibit	Categorical definitions of mobbing can be vague and behaviors or increases in intensity can straddle two or more categories creating ambiguity; difficult to compare response across species
Observations	Detailed descriptions of mobbing events	Provide a lot of information about what mobbing looks like in the observed species	Observations do not measure mobbing

The first method of measuring mobbing (presence or intensity) is recording calling behavior of mobbers. This method reflects a taxonomic study bias towards birds and

mammals, where calling is often a defining mobbing behavior and an easy one to record. Several metrics are frequently used when examining mob calls, including the number of individuals calling, (Arnold, 2000; Coomes, McIvor, & Thornton, 2019; Królikowska, Szymkowiak, Laidlaw, & Kuczyński, 2016), call type (Carlson, Healy, & Templeton, 2017b; Suzuki, 2014) call rate, (Bartmess-LeVasseur, Branch, Browning, Owens, & Freeberg, 2010; Coppinger, Kania, Lucas, Sieving, & Freeberg, 2020; Cross & Rogers, 2006), and detailed acoustic measurements (Carlson, Greene, & Templeton, 2020; Courter, Perruci, McGinnis, & Rainieri, 2020; Furrer & Manser, 2009; Ha et al., 2020; Kalb & Randler, 2019; Manser et al., 2014).

While many studies have shown how different species encode information about threat in their mobbing calls, we still know very little about whether there is individual variation in calling within a group during mobbing events (e.g., do only particular individuals call, or do all individuals call; Francis et al., 1989; Gehlbach & Leverett, 1995; Griesser & Ekman, 2005; Griesser & Suzuki, 2016). Moreover, it is unclear whether mobbing calls reflect the caller's perceived level of threat vs. the actual level of threat posed by the predator (but see: (Carlson, Greene, et al., 2020). To determine if calling reflects the actual threat or perceived threat it is necessary to look at both calling and other mobbing behaviors/contexts as some species vary their calling behavior in response to factors other than just the actual threat. For example, red-breasted nuthatches change their calling behavior to the same threat based on the source of information (Carlson, Greene, et al., 2020), while other species alter their calling behavior to the same predator differently depending on the presence of other individuals (e.g., presence of own offspring, Griesser & Ekman, 2005; presence of conspecific females, Cunha, Fontenelle, & Griesser, 2017b). This variation in calling behavior due to non-predator influences highlights why collecting data on other factors that can affect a species' vocalizations during mobbing is important, when using calls to measure mobbing behavior. This is particularly important in species with graded calls, as determining whether a call is referential or influenced by the caller's perception of threat is more difficult to assess in these species as opposed to species that use different calls for different classes or types of predators (Griesser, 2009; Suzuki, 2014).

The second approach to measure presence and/or intensity of mobbing is the closest distance prey approach the predator. This is a useful measurement as approaching the predator closely is a part of aggressive mobbing where individuals will harass and, in many cases, even attack the predator, which requires a close distance and the incurred risk in doing so. However, what constitutes as a 'close approach' can vary across species. This distance

can range from less than a meter in small animals like squirrels (Courter & Ritchison, 2010; Owings et al., 2001) to larger distances, such as 4 meters, in larger animals like giant otters *Pteronura brasiliensis* (Leuchtenberger et al., 2016). Therefore, describing a range of distances that are biologically relevant for mobbing in the target species, or including other measures of mobbing like stereotyped behaviors, would help to differentiate between predator inspection and mobbing.

Although approaching a predator and getting within a close distance is part of mobbing, approaching at farther distances (especially without secondary behavioral measures such as stereotyped movements or calling) does not allow us to separate mobbing from predator inspection. The latter has very different motivations, costs, and benefits compared to mobbing, and unlike mobbing, predator inspection is primarily used by individuals to obtain information about a (potential) predator (Caro, 2005). During predator inspection, prey do approach the predator but they do not engage in most of the conspicuous movements or calls used during mobbing. Consequently, the risk of predator inspection is much lower than during mobbing. Thus, approaching a predator very closely is almost always indicative of mobbing, though many studies use approaches at distances at which predator inspection and mobbing cannot be separated without considering other behaviors as well (e.g., 10 meters; Dutour et al., 2017; Ficken & Popp, 1996).

The third approach used to measure the presence and/or intensity of mobbing is using the number of contact (e.g., hitting, biting, etc.) or non-contact (i.e., run/fly/swim by) attacks towards the predator. Though not as common as other behaviors, attacking a predator is only found in mobbing, and therefore a useful measure. While attacks are a clear identifier of mobbing behavior, not all mobbing events escalate to include attacks, and not all species attack when mobbing. This variation in expression makes it a useful behavior in some species, but one that cannot be used in many other species.

The fourth approach uses levels of activity as a measure for the presence and/or intensity of mobbing including: approach rate/proportion (Andersen, 1990; Dutour, Cordonnier, Lena, & Lengagne, 2019), number of individuals/species participating/arriving (Arnold, 2000; Clode et al., 2000), and duration within close proximity to predator (Feeney & Langmore, 2013; Owings et al., 2001), calling rate (specifically as a proxy to measure the level of activity; Courter & Ritchison, 2012; Cross & Rogers, 2006; Dutour et al., 2021). While increased mobbing activity is a good way to capture the intensity of mobbing behavior, due to the immense variation and the lack of a standardized approach to measure mobbing

across species and contexts, this approach can be ambiguous and is not consistent across species or studies.

The fifth way to measure the presence and/or intensity of mobbing is to record the latency of response to a signal (i.e., the presentation of a predator and/or a playback, Baker & Becker, 2002; Kalb & Randler, 2019). While this is a useful measure when the focal individuals cannot miss the onset of a signal (i.e., all focal individuals are in direct sight line or hearing distance), it can be difficult to determine whether a latency to respond is due to a real lack of response or because ostensible recipients did not detect the signal.

A sixth approach includes multiple measures to create a scale of mobbing and is used to measure the intensity of a mobbing response in a categorical fashion. Unlike many other measures, this measurement is ordinal and integrates multiple measures of mobbing behavior to provide a more accurate and inclusive measurement of the complete behavior. Usually, these scales run from 'no-mobbing', through intermediate combinations of steps to physical contact with the predator, e.g., "1) an individual was > 10 m away from model making visual displays and/or giving warning calls or being silent, 2) an individual was ≤ 10 m and > 5 m away making visual displays and/or giving warning calls or being silent, 3) an individual was ≤ 5 m and > 2 m away being silent, 4) an individual was ≤ 5 m and > 2 m away making visual displays and/or giving warning calls, 5) an individual was ≤ 2 m away being silent, 6) an individual was ≤ 2 m away making visual displays and/or giving warning calls but not attacking the model, and 7) an individual was physically attacking the model." (Cunha et al., 2017b, p 1518). While this is a comprehensive and accurate way to measure mobbing behavior, many of these scales still include subjective, undefined, and/or species-specific measures that differ hugely across studies making comparative research difficult.

Finally, many observational studies and natural history reports include comprehensive descriptions of mobbing (Deng, Lee, & Wee, 2008; Hein, 1996b; Passamani, 1995) and provide a clear and useful example for the detail of information about mobbing that would allow for researchers to better be able to conduct comparative studies. Such detailed descriptions allow for a broader examination of mobbing behavior. Examples are many observational studies (Deng et al., 2008; Hein, 1996b; Passamani, 1995) that provide theories (tested or not) about the origins, development, or motivations of mobbing based on detailed descriptions (Clemmons & Lambrechts, 1992; Curio & Regelmann, 1985; Ishihara, 1987; Owings & Coss, 1977), and use these descriptions and those of other similar studies to draw parallels between multiple species allowing for broader, more generalizable conclusions.

2.2 Can and should we measure mobbing intensity?

Differences in species morphology, ecology, and local habitat structure, can influence a species' willingness to mob, what predators they mob, and what mobbing behaviors they engage in. Mobbing intensity is a useful way to understand the selective pressures, risk, and perception of mobbing species, but understanding what mobbing intensity actually means in different species or studies, can be difficult.

One source of variation that has an impact on both the propensity and expression of mobbing is a species' morphology. Different taxa have a different body design, and thus, mobbing is expressed differently across taxa. For example, mammals display characteristic ear, tail, and fur postures that are indicative of mobbing (Berger, 1979; Graw & Manser, 2007; Owings & Loughry, 1985; Owings & Owings, 1979). In some mammals, mobbing even incudes throwing of objects/substrate e.g., in rock squirrels, *Spermophilus variegatus* (Owings et al., 2001), California ground squirrels (Owings & Coss, 1977), black-tailed prairie dogs (Owings & Owings, 1979). Similarly, mobbing birds display specific wing, tail, and feather postures (Altmann, 1956; Carlson et al., 2019; Hinde, 1954a), fish display specific threat postures and methods of movement and predator approach (Donaldson, 1984; Lachat & Haag-Wackernagel, 2016), and invertebrates sting and create a heat-ball (i.e. surround a wasp as a group which can create temperatures of up to 47°C; Ono, Igarashi, Ohno, & Sasaki, 1995; Seeley et al., 1982). Even within taxa, species with different gross morphology can display different mobbing behaviors. Primates for example, often use their arms and even sticks to threaten or attack a predator (Boinski, 1988), while squirrels and other quadrupedal mammals rely on full body lunging, abrupt diagonally forward and backwards approaches and retreats or distinct tail postures (Graw & Manser, 2007; Owings & Coss, 1977; Owings et al., 2001; Owings & Owings, 1979). Notably, these differences in mobbing behavior can also affect the costs, risks, and outcomes of mobbing.

Even within a species, local ecology and habitat structure can alter mobbing behavior. For example, European pied flycatchers, *Ficedula hypoleuca,* mob more intensely in unmanaged forests than managed ones which have lower bird densities and heterospecific diversity (Hua & Sieving, 2016; Krama et al., 2011). Differences in habitat structure may also influence mobbing behaviors like 'closest approach' distance. In many bird species the degree of cover may impact how close individuals get to a predator. If there is dense cover all around a predator into which the mobbers can escape, they may be more willing to approach more closely than if a predator perches exposed with no cover nearby (N.C. and M.G. per

obs.). Similarly, lower threat situations (i.e., dense cover, larger flocks, etc.) may allow for a more energetic and risky mobbing response as seen in some call metrics in UK tit species (Carlson, Healy, & Templeton, 2020).

Some differences in mobbing intensity could also be affected by aggressiveness, as bolder, more neophilic individuals are often more aggressive mobbers (Vrublevska et al., 2014) while differences in average aggressiveness across different populations can result in very different mobbing responses (Davies & Sewall, 2016; Hardman & Dalesman, 2018). While mobbing intensity can provide important information about individual motivations, perceived risks and benefits, as well as selective pressures maintaining mobbing behavior, the lack of standardization in measuring mobbing intensity across studies and species, limits comparative work.

2.3 What do inconsistencies in quantifying mobbing mean for comparative research?

While mobbing is prevalent across the animal kingdom, we still know little about how this behavior evolved, what maintains it, and which benefits it provides. Comparative studies on mobbing would be useful to address these knowledge gaps, but our ability to compare mobbing behavior across species is limited due to differences in measurement and approaches to studying mobbing. To date, efforts to determine the evolutionary pressures that facilitate mobbing behavior have largely focused on specific communities or specific taxa (Carlson, Healy, et al., 2017b; Crofoot, 2012; da Cunha, Fontenelle, & Griesser, 2017a; Gottfried, 1979; Hua & Sieving, 2016; Manser et al., 2014).Studying specific communities provides useful insights to mobbing prevalence and species characteristics among those communities, however, many of these studies are limited in their conclusions. First, most of these studies do not clearly differentiate between a mobbing response and predator inspection (Dutour et al., 2017; Ficken & Popp, 1996; see above). Second, while several studies do consider multiple sources of variation in mobbing, most studies only include a subset of important sources (e.g., predator threat, season, *or* habitat structure) and thus result in a potentially inaccurate measure of mobbing propensity and/or intensity. These shortcomings inflate the occurrence of false negatives, for example, the number of species that are classified as non-mobbers when, in fact, the conditions were not ones in which a focal species mobs (e.g., the type of predator used, time of year, degree of cover). Thus, studies conducted during a single season risk excluding any species that mob only during the breeding season or the non-breeding season but not both (Lima, Casas, Ribeiro, Souza, & Naka, 2018; Motta-Junior & Santos-Filho, 2012; Pawlak, Kwieciński, & Hušek, 2019). Similarly, if only one

type (e.g., hawk *or* owl) or size (e.g., small raptor *or* large one) of predator (Lima et al., 2018; Pawlak et al., 2019) is presented, then species that mob predators of different types or sizes may also be mis-categorized. If a predator is a risk for only some species but not others (da Cunha et al., 2017a), then those species at less risk may be classified as non-mobbers, even if they do reliably mob a predator that is more risky for them.

A focus on specific taxa (e.g., Paridae), or several taxa in one area (e.g., local mixed-species flocks) can provide useful insights into specific traits that may facilitate mobbing behavior or explore the variation of mobbing behavior in similar species while controlling for phylogeny, or habitat. However, studies focusing so narrowly (often only examining closely related species that are either sympatric or live in similar habitats and share similar life histories (Carlson, Healy, et al., 2017b; Coppinger et al., 2020; Gursky & Nekaris, 2007; Manser et al., 2014; Templeton & Greene, 2007), can reduce the effectiveness of this approach. For example, by focusing on only a few species, studies can overlook other species involved in mobbing events (e.g., focusing only on Paridae in mixed-species mobbing) or by focusing on only one habitat type (e.g., focusing only on species found in temperate habitats) studies can overlook ecological factors that can alter mobbing responses.

3. WHAT IS THE FUNCTION OF MOBBING?

Not only is the definition of mobbing variable, the function of mobbing (i.e., how this behavior benefits individuals that engage in it) remains contentious. Indeed, Curio (1978) proposed ten different hypotheses as to the purpose of mobbing. Subsequent research has shown that the function of mobbing is probably a combination of more than one of these hypotheses (Figure 2). Additionally, due to their inherent interconnectedness, multiple hypotheses often are not separable from one another or provide similar outcomes (i.e., different motivations for mobbing result in the same beneficial outcome; Figure 3). These original 10 hypotheses, and four more recently proposed hypotheses, can be broken down into four main general benefits/categories as to how they help a mobbing individual: (i) physically remove the predator, (ii) disrupt the predator hunting behavior, (iii) communicating with other potential prey, and (iv) non-predator related benefits.
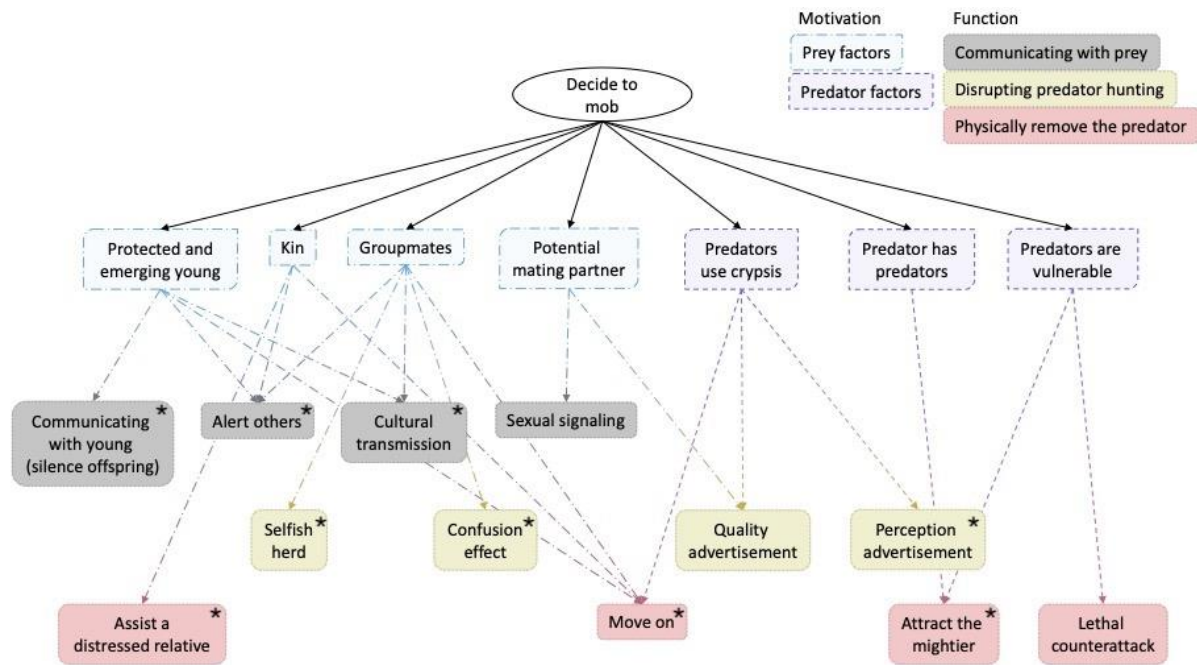
Figure 3 The interconnections of the motivations and functions of mobbing based on the different mobbing hypotheses. When deciding to mob, individuals can have one or more different motivations concerning other prey or the predator, which in turn can serve a number of different functions with similar outcomes.

3.1 Hypotheses regarding the function of mobbing

3.1.1 Physically remove the predator

Three hypotheses focus on how mobbing can remove the predator from the area, either through moving-on, injury, or death.

The 'move on' hypothesis

The *move on* hypothesis posits that mobbing behavior will cause a predator to change movement patterns (Bildstein, 1982), leave an area sooner (Clark, 2005), fly farther away (Pettifor, 1990), and perhaps even avoid an area in future (Pavey & Smyth, 1998), especially as the intensity or duration of the mobbing event increases (Curio & Regelmann, 1985; Flasskamp, 1994). This function of mobbing is one of the most widely accepted with evidence of fewer mobbing species in the predator's diet (Ekman, 1986; Pavey & Smyth, 1998), avoidance of areas that contain mobbing prey by predators (Pavey & Smyth, 1998), predators altering their spatial movement patterns to avoid mobbing species (Bildstein, 1982; Clark, 2005; Pettifor, 1990), and stress and escape behaviors shown by predators being mobbed (Consla & Mumme, 2012; Curio & Regelmann, 1985).

Attract the mightier

The *attract the mightier hypothesis* posits that mobbing behavior and/or calls of prey species will attract a predator that preys on the predator species that is being mobbed, and thereby removes the threat (Grim, 2007). We are aware of three studies that have examined this hypothesis (Fang et al., 2020; Grim, 2007; Gursky, 2006), with one showing some support (Fang et al., 2020).

Lethal counterattack

The *lethal counterattack hypothesis* posits that the act of mobbing will kill the predator, thereby removing the threat. There are multiple field observations of prey mobbing and killing their predators including in primates (Crofoot, 2012), honeybees (Ono et al., 1995), raptors (Lourenço, Penteriani, Delgado, Marchi-Bartolozzi, & Rabaça, 2011), and fasciated antshrikes, *Cymbilaimus lineatus,* Chiver, Jaramillo, & Morton, 2017) At least one experimental manipulation showed that raptor species preyed upon by eagle owls, *Bubo bubo*, mob eagle owls with lethal intent, by attacking the head and neck with talons, thought to be a deliberate attempt to kill the intra-guild predator (Lourenço et al., 2011).

3.1.2 Disrupting predator hunting strategy/advantage
The 'selfish herd' & 'confusion effect' hypotheses

The *selfish herd* and *confusion effect hypothesis* posits that mobbing in a group (especially a group that is made up of individuals roughly similar in size and shape) decreases the chance that any one mobbing individual will be caught by the predator (Caro, 2005; da Cunha et al., 2017a; Foster & Treherne, 1981; Hamilton, 1971). In the *selfish herd hypothesis* this is achieved by numerical dilution of the risk (i.e., the more individuals that mob, the lower chance any one individual is killed). In the *confusion effect hypothesis* this is achieved through effects of increasing group size reducing the predator's ability to target a specific individual.

While it is not always easy to determine whether a reduction in predator threat is due to a selfish herd or a confusion effect, there is evidence that predators are less successful when hunting individuals in groups, though not of mobbing groups in particular (Caro, 2005; Foster & Treherne, 1981; Hogan, Hildenbrandt, Scott-Samuel, Cuthill, & Hemelrijk, 2017; Kenward, 1978).

Pursuit deterrent ('perception advertisement' and 'quality advertisement' hypotheses)

The *pursuit deterrent hypothesis* posits that the mobbing signals themselves persuade the predator to give up hunting that prey (Caro, 2005; Frankenberg, 1981; Smythe, 1970). In the *perception advertisement hypothesis*, the prey signals that it has detected the predator, and thus an attack is likely to fail as the prey is alert, close to cover, or can otherwise evade a potential attack. In the *quality advertisement hypothesis*, the signal indicates that the prey's high quality (i.e., agility, strength, etc.) means that they can outrun/escape from the predator's attack. Though few studies have examined mobbing in this specific context, there is some support for the pursuit deterrent function of mobbing in Scurids (Clark, 2005). When being mobbed by Scurids, snakes are more likely to leave an area, but only when hunting; resting snakes do not respond to mobbing Click or tap here to enter text.(Clark, 2005; Cresswell, 1994a; FitzGibbon & Fanshawe, 1988; Gursky, 2006).

Aiding a distressed relative

The *aiding a distressed relative hypothesis* is only applicable when an individual is already caught by a predator. It predicts that mobbing the predator that has caught a relative or group member will distract the predator, allowing the captive individual to escape. Mobbing a predator that has caught a group/family member has been observed in the wild (Crofoot, 2012; Jack et al., 2020) and predator mounts with 'captured' prey (both dead and alive) are used to elicit mobbing behavior in prey (Barash, 1976; Carlson, Pargeter, & Templeton, 2017; Chu, 2001). Mobbing events elicited by mounts with 'captured prey can be more intense than when encountering a predator alone (e.g., larger mobbing groups, louder mobbing calls, more swoops at the predator (Barash, 1976; Conover, 1987; Crofoot, 2012; Jack et al., 2020).

3.1.3 Communication with other prey to reduce their risk of being caught

There are a few hypotheses focusing on how communicating with others (often kin or conspecifics, but also heterospecifics) will decrease an individual's chance of being caught by a predator. These hypotheses all predict that mobbing produces a signal or information that increases a receiver's chance of survival.

Alerting others hypothesis

The *alerting others hypothesis* posits that mobbing signals a danger to others in the vicinity, allowing them to take appropriate action before they have seen the predator, thereby

increasing their chance of survival (Carlson, Healy, & Templeton, 2018; Colombelli-Négrel, Robertson, & Kleindorfer, 2010; Suzuki, 2011, 2015). Individuals are more likely to mob a predator in the presence of kin (Colombelli-Négrel et al., 2010; Gehlbach & Leverett, 1995; Graw & Manser, 2007; Griesser, 2009; Griesser & Ekman, 2005; Tamura, 1989), (potential) breeding partners (Cunha et al., 2017b; Gehlbach & Leverett, 1995; Krams, Krama, & Iguaune, 2006), or familiar individuals (Grabowska-Zhang, Sheldon, & Hinde, 2012; Krams & Krama, 2002; Krams, Krama, & Iguaune, 2006a and b). More evidence in support of this function comes from the response of mobbing call recipients. Recipients frequently respond to mobbing calls with increased alert behavior/posture, which should increase survival if a predator were to attack (Dutour & Danel, 2020; Graw & Manser, 2007; Ito & Mori, 2010). While some evidence shows that individuals may signal to heterospecific prey (Goodale & Kotagama, 2006), the same functional response may occur when others simply listen to this broadcast signal, regardless of the intended recipient (Templeton & Carlson, 2019). Certainly, many heterospecifics do listen to the information in mobbing calls (Carlson, Greene, et al., 2020; Carlson, Healy, et al., 2020; Coppinger et al., 2020; Ito & Mori, 2010; Munoz, Brandstetter, Esgro, Greene, & Blumstein, 2015; Templeton & Greene, 2007) and these calls may facilitate the formation of many mixed-species-flocks (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Goodale & Kotagama, 2008; Goodale & Ruxton, 2010; Sridhar, Beauchamp, & Shanker, 2009; Sridhar, Jordán, & Shanker, 2013).

Communicating with young

The *communicating with young hypothesis* is similar to the *alerting others hypothesis* but focuses on the mobber's dependent offspring (i.e., nestlings, fledglings, cubs, etc.). It posits that by mobbing, a parent will decrease the risk that their offspring are depredated by inducing a beneficial change in the behavior of those offspring. When hearing their parents' mobbing calls, nestlings of many bird species will become silent (e.g., Eastern bluebirds, *Sialia sialis,* Grabarczyk & Ritchison, 2015, and red-winged blackbirds, *Agelaius phoeniceus,* Knight & Temple, 1988), crouch down (Japanese tits, *Parus minor,* Ha et al., 2020; Suzuki, 2011, and Eastern bluebirds, Grabarczyk & Ritchison, 2015), force fledge (Japanese tits, Ha et al., 2020; Suzuki, 2011), or engage in other anti-predator behaviors that reduce their risk of being eaten, even if they have never seen the predator (e.g., Japanese tits, Ha et al., 2020; Suzuki, 2011). In many species, these behavioral responses to parents' mobbing calls change as the young develop, and more adult-like responses become more effective (e.g., respond by mobbing after developing the dexterity to escape a predator should

it become necessary; (Hinde, 1954a, 1954b, 1961; Suzuki, 2011). Parents also often show peaks in mobbing activity when young are particularly vulnerable (Cully & Ligon, 1986; Curio, 1975; Freeman & Miller, 2018; Graw & Manser, 2007; Shedd, 1982, 1983; Tamura, 1989).

Cultural transmission (predator and place)

The *cultural transmission hypothesis* focuses on learning about a predator or place. It posits that by observing mobbing, naïve individuals will learn something about either the predator itself or the place it often occurs. This then allows them to avoid the predator or place in the future. Many species seems to learn about novel predators by observing or hearing a mobbing event in conjunction with a novel stimulus (Baker, 2004; Curio, Ernst, & Vieth, 1978a; Griffin & Jr, 2005; Vieth, Curio, & Ernst, 1980), and naïve juveniles that observed mobbing of a main predator (goshawk, *Accipiter gentilis*) were more likely to survive the winter than those that did not, suggesting that they learned to avoid goshawks (Griesser & Suzuki, 2017). While evidence supports the cultural transmission of predator threat information, not all species have shown this ability (Campbell & Snowdon, 2009). However, it remains untested if individuals can also learn about dangerous places (i.e., where predators frequently occur). However, there is evidence that individuals may learn about dangerous places, at least in the short term. Peters' monocle bream, *Scolopsis affinis*, for example, will avoid foraging near a Bobbit worm, *Eunice aphroditois*, (a very dangerous but stationary ambush predator) once it has been discovered and mobbed (Lachat & Haag-Wackernagel, 2016).

3.1.4 Non-predator related hypotheses
Signaling quality to potential breeding partners

The *sexual signaling hypothesis* posits that individuals can indirectly show off their quality (e.g., mobility, boldness) by successfully avoiding being eaten during mobbing (Zahavi, 1977). One study has provided support for this hypothesis: males of several bird species increase their mobbing intensity in the presence of conspecific females, particularly when mobbing a more dangerous predator (Cunha et al., 2017b). However, it is not clear whether bolder or more frequent mobbers father more chicks or are in better condition than others (Cunha et al., 2017b).

Mobbing mimicry

Multiple species do mimic heterospecific mobbing calls and there are different hypotheses for why species do so. Some species may mimic mobbing calls to attract heterospecifics. For example, thick-billed euphonias, *Euphonia laniirostris*, will mimic the alarm call of a yellow-green vireo, *Vireo flavovirids*, when encountering a predator, causing neighboring vireos to assist in mobbing (Morton 1976 in Chu, 2001). Similaraly, brown thornbills, *Acanthiza pusilla*, mimic heterospecifics mobbing calls when mobbing predators to attract heterospecific assistance and to deflect terrestrial predators from depredating their nest (Igic & Magrath, 2014). In contrast, greater racket-tailed drongos, *Dicrurus paradiseus*, mimic mobbing calls of multiple species all at once in the absence of predators, to draw mixed-species flocks to them so they can join the mixed-species flock (Goodale, Ratnayake, & Kotagama, 2014). Finally, some species mimic mobbing calls to distract conspecifics. Superb lyrebird, *Menura novaehollandiae*, males mimic multi-species mobbing events during and shortly after display and mating with females, to prevent females from leaving the display area or to prolong mating to ensure a better chance of success (Dalziell, Maisey, Magrath, & Welbergen, 2021).

3.2 Links among mobbing hypotheses and potential evolutionary drivers for mobbing

While mobbing has many different functions, these functions are often interconnected, and multiple functions can be achieved in one mobbing event, or multiple functions can be intended by the mobber. Both removing the predator and communicating with others (kin, heterospecifics, the predator) tend to occur in all mobbing events, suggesting a likely primary function and an evolutionary path for mobbing to emerge. However, there remain other more specific functions that likely evolved from these main functions or from each other making it difficult to understand/measure the motivations of a mobber. One way to discuss the links between these different functions is in the context of potential evolutionary trajectories in both defence of young (i.e., mobbing in any protected area where parents raise young – e.g., nest, burrow, den) and non-young defence contexts.

When contemplating the function of mobbing calls in the young defence context, both silencing offspring and removing the predator (to reduce the potential risk to offspring) are likely primary intended functions, and ones that may have driven the evolution of mobbing. In birds, begging calls are a conspicuous signal that can draw attention to the nest, and provisioning is one way to silence these conspicuous signals (Magrath, Haff, Horn, & Leonard, 2010; McDonald, Wilson, & Evans, 2009). Quieter nests (i.e., ones in which adults

silence offspring) are more likely to fledge more offspring as they are less likely to be discovered by nest predators (McDonald et al., 2009). When encountering predators near the nest or den, many species have a variety of predator defence behaviors including mimicking a dangerous animal (hissing), leading a predator away (distraction display), and attacking the predator (mobbing, Caro, 2005). The latter may have arisen as part of a suite of different nest defence behaviors and increased aggression towards intruders, specifically predators. After mobbing was established as an effective anti-predator strategy against nest predators, secondary functions may have evolved. Cultural transmission, for example, may have been one of these secondary functions. Parents frequently use communication (with their offspring, their mate, and/or the predator) during mobbing, which could lead to communication about different predators (Figure 2). Over time this could lead to associative learning and cultural transmission of predator identity or threat.

When contemplating the functions of mobbing in non-young defence contexts, removing the predator or perception advertisement are the likely primary functions. However, unlike in the nest-defence context, this function likely evolved as an escalation to predator inspection. Although different, there are many similarities in predator inspection and mobbing (Figure 1), and predator inspection can escalate into mobbing, but the reverse is not true (Figure 1). Individuals who engage in mobbing or predator inspection can obtain more information about predators. However, the importance of information acquisition likely differs between these behaviors. In predator inspection, information acquisition is the primary motivation, while in the case of mobbing, individuals must have already obtained a large amount of information about the predator before deciding whether or not to mob, suggesting that information acquisition is a secondary or negligible motivation for mobbing.

In both predator inspection and mobbing, perception advertisement is a common function as prey often (predator inspection) or always (mobbing) include some stereotyped signals that can alert the predator to their discovery, but are non-threatening (e.g., orienting towards the predator and 'watching' them, approaching and retreating, posture changes; (Carlson et al., 2019; Carlson, Pargeter, et al., 2017; Caro, 2005; Fishman, 1999; FitzGibbon, 1994). For many predators this alone can deter hunting for a period of time (Caro, 2005), but for those where signaling to the predator is not enough, escalation of aggression (mobbing) could be more effective. Similar to young defense contexts, mobbers are signaling to multiple receivers (the predator, conspecifics, heterospecifics) meaning that alerting/informing others may be a secondary function of mobbing.

The prevalence of communicating with others (including the predator) in all mobbing contexts may be an important driver of further mobbing functions as it plays in important role in attracting the mightier (communicating with other predators), cultural transmission (communicating with kin and heterospecifics), quality advertisement (communicating to the predator), sexual signaling (communicating to conspecifics), and confusion or selfish herd effects (communicating/recruiting conspecifics and heterospecifics; Figure 3). To truly understand the relationship between the functions of mobbing and the evolutionary pressures that gave rise to mobbing behavior, it is necessary to compare mobbing across populations, species, and taxa.

3.3 Mobbing motivation and behavioral outcomes

To try and understand the drivers, costs, and benefits to mobbing behavior, it is important to understand both the motivation individuals have when choosing to mob (i.e. what mobbing function they use), and the results of their behavior. However, the interconnectedness of mobbing functions creates ambiguity when trying to determine the motivation that causes an individual to engage in mobbing behavior. This is because mobbing is often driven by a number of different factors based on both prey and predator life history and ecology (Figure 3). Additionally, the anticipated outcomes of mobbing may be diverse (Figure 3). For example, although an individual's primary motivation may be to signal to their groupmates to alert them that a predator is present (alert others), this may also serve to recruit others thereby lowering the likelihood of being killed (selfish herd, confusion effect), provide a demonstration to naïve individuals of a threatening predator (cultural transmission), and force the predator to leave the area (move on). Conversely, if an individual's mobbing decision functions to alert others, the signal may have been aimed at one group in particular (e.g., young) even though many other individuals also received the signal (kin, groupmates, the predator). These multiple links between motivation/target audience and the functions of mobbing create a problem for researchers when trying to understand the driving motivations and desired outcomes that result in an individual mobbing in any given circumstance. However, by examining mobbing behavior in multiple contexts, species, and taxa, stronger patterns of use and motivation may emerge, allowing for a better understanding of individual motivations for mobbing.

4. MOBBING AS A PROXY FOR 'COGNITION'

While mobbing is a fascinating anti-predator behavior on its own, 40.6 % of studies (Table 1) use the mobbing response as a proxy to understand cognitive processes. This work typically addresses predator recognition/categorization, information encoding/language-like adaptations, and learning.

Mobbing is frequently used as a proxy to study cognitive processes as it is a useful tool. Its graded behavioral response that differs among predator types, and threats allows for straightforward experiments that ask the focal individual how *they* perceive the predator, making it useful for experiments addressing predator recognition and categorization. Different species can and do differentiate between different predators within and between taxonomic categories (Griesser, 2009; Suzuki, 2014, 2018; Templeton, Greene, & Davis, 2005), predator behaviors and states (Griesser, 2008), and which predator features, if any, they use to make some of these differentiations (i.e., yellow eyes, talons, chest barring, etc.; Beránková, Veselý, & Fuchs, 2015; Beránková, Veselý, Sýkorová, & Fuchs, 2014; Curio, 1975; Davies & Welbergen, 2009; Němec et al., 2014; Trnka, Prokop, & Grim, 2012). Mobbing calls are also often used to determine the perception of caller reliability with respect to their recognition and response to predators (Carlson, Greene, et al., 2020; Carlson, Healy, et al., 2020; Cunha & Griesser, 2021; Woods, Kings, McIvor, & Thornton, 2018)

Similarly, mobbing can be a useful tool to study language-like adaptations and information encoding. Like song, the standard for studying language-like vocal behavior in the animal kingdom, mobbing calls are usually made up of discrete elements and/or note types (Campbell & Snowdon, 2007; Carlson, Healy, et al., 2017b; Graw & Manser, 2007; Suzuki, 2014; Templeton et al., 2005), can contain many different combinations (Suzuki, 2014), and show syntax (Engesser, Ridley, & Townsend, 2016; Suzuki, 2021; Suzuki, Wheatcroft, & Griesser, 2017, 2016; but also see: Clucas, Freeberg, & Lucas, 2004; Dutour, Lengagne, & Lena, 2019; Freeberg & Lucas, 2002, 2012; Hailman & Ficken, 1986; Lucas & Freeberg, 2007; Suzuki, 2021). Mobbing calls also can be functionally referential (Griesser, 2008; Suzuki, 2018) and include graded information related to internal or external conditions and threat (Bartmess-LeVasseur et al., 2010; Carlson, Greene, et al., 2020; Graw & Manser, 2007; Griesser, 2009; Sieving, Hetrick, & Avery, 2010; Templeton et al., 2005). Experimental manipulations of the perceived threat and type of predators have been used to determine the information individuals encode in their mobbing calls (Courter & Ritchison, 2010; Graw & Manser, 2007; Griesser, 2009; Suzuki, 2012, 2014; Templeton et al., 2005),

how much of this information is understood by both conspecifics and heterospecifics (Carlson, Greene, et al., 2020; Hetrick & Sieving, 2011; Huang, Sieving, & Mary, 2012; Magrath et al., 2014; Templeton & Greene, 2007), and how individuals encode information in their calls (Carlson, Greene, et al., 2020; Carlson, Healy, et al., 2017b; Griesser, 2009; Suzuki & Ueda, 2013; Templeton et al., 2005)

Finally, mobbing can also be a method for studying learning. Though the stereotyped behavior and calls exhibited during mobbing can be innate in some species, many species have shown that the association between mobbing behavior and a predator threat is learned (Baker, 2004; Carlson, Healy, et al., 2017a; Curio, Ernst, & Vieth, 1978b; Curio et al., 1978a; Griesser & Suzuki, 2017; Vieth et al., 1980). To this end, the use of exposure to a new stimulus alongside a simulated mobbing event has shown that individuals can learn to recognize new predators or new mobbing calls (Griffin, 2004), what aspects of mobbing are needed to make these new connections (Griffin, 2004), and the degree to which new information about novel or known stimuli can override personal experience (Curio et al., 1978a; Vieth et al., 1980).

Nonetheless, we still lack an understanding of many fundamental aspects of mobbing. It remains unclear which ecological conditions that produced and maintain this behavior, the sources of variation (outside predator threat) in this behavior, and the prevalence of this behavior. Thus, conclusions based on mobbing response that do not take these factors into account may inadvertently misinterpreted. Additionally, frequently only one aspect of this behavior (e.g., mobbing calls) is measured, which could result in misinterpretation of mobbing response. In some species, vocal and behavioral measures of mobbing differ based on mobbing stimulus or condition (e.g., the source of the information, Carlson, Greene, et al., 2020, or the reliability of the signaler, Cheney & Seyfarth, 1988; Silvestri, Morgan, & Ridley, 2019). Not just the signal itself matters, but the learner's state can also have a substantial impact on learning (Griffin, 2004), suggesting that a lack of learning may simply indicate that the conditions for learning have not been met. Thus, a better understanding and quantification of the behavior itself, will help to create a solid base from which to continue asking more targeted and detailed questions.

5. CONCLUSIONS AND MOVING FORWARD

Approaching mobbing in a more standardized way would allow for more comprehensive comparative analyses. Here we identify four major areas of research for

investigation: 1) factors that influence mobbing behavior (aside from threat), 2) taxonomic bias, 3) cost-benefit explorations, and 4) responses to anthropogenic changes.

5.1 Standardization and quantification of mobbing

A clear and consistent use of an inclusive mobbing definition that accounts for differences in mobbing behavior across taxa, but remains sufficiently specific to rule out behaviors with different motivations, costs, and benefits, such as predator inspection would provide the detail and standardization necessary to allow for comparative studies and a more global view of mobbing. To this end we suggest the following mobbing definition: "an anti-predator behavior where preyed-upon species approach and harass a predator while displaying conspicuous, stereotyped movements and/*or* vocalizations". By including harassment of a predator, we can separate mobbing from predator inspection and other young defense strategies (e.g., distraction displays). By including conspicuous, stereotyped movements and/*or* vocalizations, we also include non-vocal mobbing species. The 'conspicuous' part of the definition again helps to separate mobbing from predator inspection.

A comprehensive definition of mobbing will ensure that we can better understand what mobbing entails and its diversity across different species. To facilitate comparative work, and a clearer understanding of mobbing across species, future work on mobbing behavior (even just aspects of the behavior, e.g., the calls), should include both a standardized description of that species' mobbing behavior and how those behaviors were measured. This standardized approach would allow for comparisons across studies and taxa, which will make comparative mobbing studies more straightforward. This, in turn, would lead to more comprehensive data across taxa allowing for studies to better address questions regarding the variation in the expression of mobbing behavior across species and taxa, the evolutionary drivers that gave rise to mobbing behavior, and the ecological conditions that maintain it. We have, therefore, created an inclusive definition that will allow both standardization and flexibility across multiple species. By employing this standardized approach (i.e., inclusive definition and standardized reporting of mobbing behavior; Supplementary Table 2) much of the subjectivity that limits comparative studies should be removed and would allow for a better understanding of what exactly constitutes mobbing behavior.

5.2 Areas requiring further investigation

5.2.1 Other factors affecting mobbing

While it is difficult to control for all factors that influence mobbing in the same study, understanding how non-predator sources of variation affect mobbing would provide a better understanding of the benefits and costs of mobbing and under what circumstances it is an effective anti-predator strategy. This in turn would elucidate the circumstances under which this behavior may have evolved, and which ecological and life-history conditions maintain this behavior across species. For example, by determining why some species only mob during the nestling period as part of nest defense behavior, while others mob year-round, we may be able to better understand the role of young-defense and self-defense for its evolution. By determining which individuals in a group (e.g., age, sex) or between groups (heterospecifics) invest most in mobbing, we may be better able to determine the costs and benefits of mobbing at the individual and group level. This knowledge could help explaining intra and inter-species differences in mobbing investment, and further clarify the ecological conditions that maintain this behavior across species and taxa.

5.2.2 Costs and benefits

Few studies have examined the costs and benefits of mobbing. However, costs and benefits are critical to understand the selective forces that facilitate the expression and evolution of mobbing. Short and long-term costs and benefits of mobbing that can be investigated can include costs such as rates at which mobbing individuals are injured or killed during mobbing events, the energetic expenditure mobbing requires, whether mobbing results in post-mobbing increases in predation, or benefits such as how effectively mobbing removes predators, whether mobbing results in long-term reduction in predation for mobbing species, or whether naive juveniles learn about novel predators and better avoid them when they disperse.

5.2.3 Taxonomic bias

Current studies on mobbing show a large taxonomic bias towards birds and mammals (Table 1). This bias limits our understanding of how widespread mobbing is, how different habitats, life-histories, and morphology influence a species' propensity to mob, under what conditions mobbing evolved, and what ecological pressures maintain this behavior across species today.

5.2.4 Mobbing and anthropogenic change

Finally, the impact of human activities on animal behavior, communication, abundance and distribution is becoming more and more apparent. Mobbing as an anti-predator strategy is

thought to be vital for many species and communities to survive. However, as the effects of anthropogenic change on animal behavior continue to come to light, it has become apparent that, like with many other aspects of animal behavior, mobbing may be heavily impacted in a number of ways. For example, mobbing calls are less effective in noisy areas (Grade & Sieving, 2016; Templeton, Zollinger, & Brumm, 2016), and changes in habitat structure lower mobbing intensity (Hua & Sieving, 2016; Krama et al., 2011) due to changes in habitat structure altering associated risk or local communities. However, these changes provide an opportunity to both better understand the benefits, costs, and risks associated with mobbing, and to find solutions to mitigate anthropogenic changes to the environment by asking questions about how these anthropogenic impacts are causing changes to animal behavior (Grade & Sieving, 2016; Templeton et al., 2016).

5.3 Summary and overall conclusions

Mobbing is an important anti-predator strategy used by an astounding number of species across taxa. However, for all its prevalence and importance, the behavior (excluding vocalizations) remains largely understudied. Along with using a more inclusive and standardized definition and documenting scheme when researching mobbing behavior, we need to turn our attention to these understudied areas. For example, targeting future studies to determine the prevalence of mobbing across taxonomic groups, establishing a concrete understanding of the actual costs and benefits associated with mobbing (e.g., energetic costs, proportion decrease of predation attempts), and establishing how specific non-predator factors (e.g., group size, presence of females, degree of cover, seasonality) affect mobbing across a range of species. By addressing the above questions, we can better understand the evolutionary drivers that gave rise to mobbing and the social and ecological conditions that maintain it. With this understanding we can then expand our knowledge of how anthropogenic change is impacting mobbing and its community-wide ramifications.

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