Mobbing in animals: a thorough review and proposed future directions

Nora V Carlson 1, 3; Michael Griesser 2-4

1) The Hakubi Center for Advanced Research, Kyoto University, Kyoto, Japan
2) Department of Biology, University of Konstanz, Konstanz, Germany
3) Department of Collective Behavior, Max Planck Institute of Animal Behavior, Konstanz, Germany
4) Center for the Advanced Study of Collective Behavior, 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 predators, warn others, and communicate about the predator's threat. While this behavior has been of interest to humans since antiquity, and aspects of it 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 ubiquitous anti-predator behavior. In this review, we explore what mobbing is, how it is used, what its functions are thought to be, its use as a proxy for cognition, before providing suggestions for specific future avenues of research necessary to improve our understanding of mobbing in its ecological and evolutionary context.

Keywords: mobbing, anti-predator behaviors, review, fish, birds, mammals, insects, reptiles

1. INTRODUCTION

Mobbing, a behavior where prey approach, harass and sometimes attack a predator, is a prevalent anti-predator behavior observed across lineages (Figure 1). While this behavior appears to be a vital anti-predator strategy for many species, the behavior itself, as well as its evolution and function remain poorly understood. In this review, we outline the current state of knowledge and highlight important gaps in our knowledge. First, we explain what mobbing entails and detail its natural history. From there, we move on to discuss how mobbing is quantified in research and what this means for comparative studies. Then, we outline Curio's hypotheses regarding the function of mobbing and discuss how these hypotheses are interconnected. We explore how mobbing may have evolved based on these interconnections and how different mobbing motivations result in similar behavioral outcomes. Finally, we call for a standardization of mobbing definitions and develop a template to allow for better quantification across studies. We end by outlining and discussing areas requiring further investigation, including the influence of other factors on mobbing, the evolution and expression of mobbing, costs and benefits of mobbing, taxonomic bias in mobbing studies, and the importance of understanding the effects of anthropogenic change on mobbing behavior.

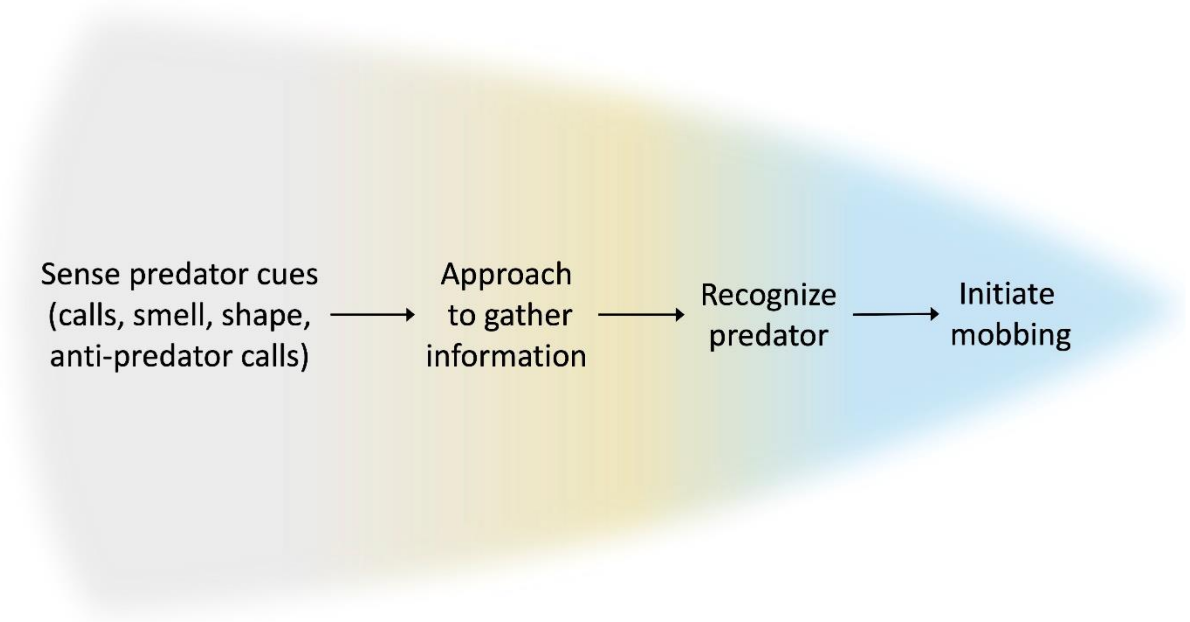

Figure 1. Progression of behavior from detecting a predator to mobbing it.

1.1 What do we know about mobbing? An overview

1.1.1 What is mobbing?

Mobbing behavior, defined as when prey (one or more) approach and harass a predator (see below for a comprehensive definition), has been a topic of interest for 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 so they could catch them (Morris, 2009, p. 167 for image) and in Aristotle's writings on nature (Aristotle, 350 BCE). One of the first mentions of mobbing behavior in the scientific literature is in a paper by Grinnell: "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) not providing any further details. In the past 70 years, mobbing behavior has been studied widely across different areas of behavioral and ecological research and is often used as a proxy to investigate aspects of predator-prey dynamics to communication, learning, and cognition (Table 1). However, although mobbing is widely prevalent across taxa, the research focus tends to be on the vocal aspects of mobbing, leaving the non-vocal aspects (e.g., body posture) largely unstudied (e.g., Altmann, 1956; Curio, 1975; Gottfried, 1979; Ishihara, 1987; Owings & Owings, 1979a). In this review, we will discuss what mobbing entails, and how it has been defined and classified across taxa, how we measure and quantify mobbing behavior, what the function of mobbing is, and how mobbing is used as a proxy for cognition, before discussing future directions and how to overcome the current limitations and move forward.

Table 1: Table showing breakdown of mobbing research literature into a) the taxa represented, b) whether it provides a definition of mobbing, c) whether it provides a detailed description of mobbing behavior in the studied species, d) what the focus of the paper was 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 = 314 papers.

	Paper contents	Number of papers
a)	Taxa studied	
	Birds	230
	Mammals	56
	Fish	14
	Insects	4

Reptiles	2
b) Provides a definition of mobbing	
Yes	124
No	190
c) Provides a detailed description of mobbing	
Yes	99
No	215
d) Paper focus	
Communication	57
Cognition	50
Mobbing	48
Descriptive	159
e) Paper type	
Experimental	233
Observational/descriptive	44
Review/theoretical	14

1.2 How to define and describe mobbing?

1.2.1 Mobbing behavior

Many scientists who study mobbing can easily differentiate it from other behaviors. However, many definitions used in the literature are very rudimentary, for example “when a prey moves toward and harasses a predator” (Dutour & Randler, 2021, p. 1) while some researchers provide specific definitions: “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)”. Although mobbing occurs in almost every animal taxon (birds, mammals, fish, insects; Table 1), it is best studied in birds due to their conspicuous mobbing behavior. Thus, roughly 73.3% of papers focused on mobbing using birds as a study system followed by studies on mammals (17.8%), fish

(4.5%), insects (1.3%), and reptiles (0.6%; Table 1). This taxonomic bias is likely a key reason why emitting “loud calls” is included in many mobbing definitions. However, not all taxonomic groups are equally likely to give loud calls (e.g., insects less likely give loud calls than 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).

When it comes to describing physical mobbing behavior, information gets even scarcer. Few studies (39.5%) define what mobbing is while even fewer (31.5%) explicitly describe what mobbing in their study species looks like (Table 1), which limits the assessment of what the author considers mobbing behavior and how a species exhibits mobbing behavior. This, in turn, makes comparative work and recognizing mobbing behavior difficult. Mobbing in different species can range hugely, from behavior such as observing and calling from a distance (e.g., in giant otter, *Pteronura brasiliensis,* Leuchtenberger, Almeida, Andriolo, & Jr, 2016*;* or dunnocks, *Prunella modularis,* NC pers obs.) to aggressive physical contact with a predator (e.g., in red-winged starlings, *Onychognathus moriom* Curio & Regelmann, 1985; or black bass, *Micropterus sp.,* Dominey, 1983). In general, mobbing is thought to primarily remove predators and/or warn others about the presence of predators. In light of this function, mobbing involves several key behaviors including: fixating on and approaching a predator, engaging in aggressive, stereotyped, movements or postures, and often moving towards and away from the predator in rapid bursts. Some, but not all, species will also produce specific vocalisations and/or physically attack the predator often by diving at (birds, Clode, Birks, & Macdonald, 2000), hitting (primates, Boinski, 1988), biting (fish, Hein, 1996), or stinging (insects, Seeley, Seeley, & Akrathanaku, 1982) them. While some specific stereotyped behaviours are unique to certain lineages, 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 proximately arise from the conflicting desire to both approach and flee the predator (Hinde, 1954a). In other lineages, 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 (insects, Kastberger, Weihmann, Zierler, & Hötzl, 2014). Providing a comprehensive description of mobbing behavior, also in studies that do not entirely focus on mobbing, can help readers understand how this behavior varies within the species (Figure 2), and how it compares to mobbing in other species within or across lineages, allowing for greater synthesis and understanding of the drivers of this behavior.

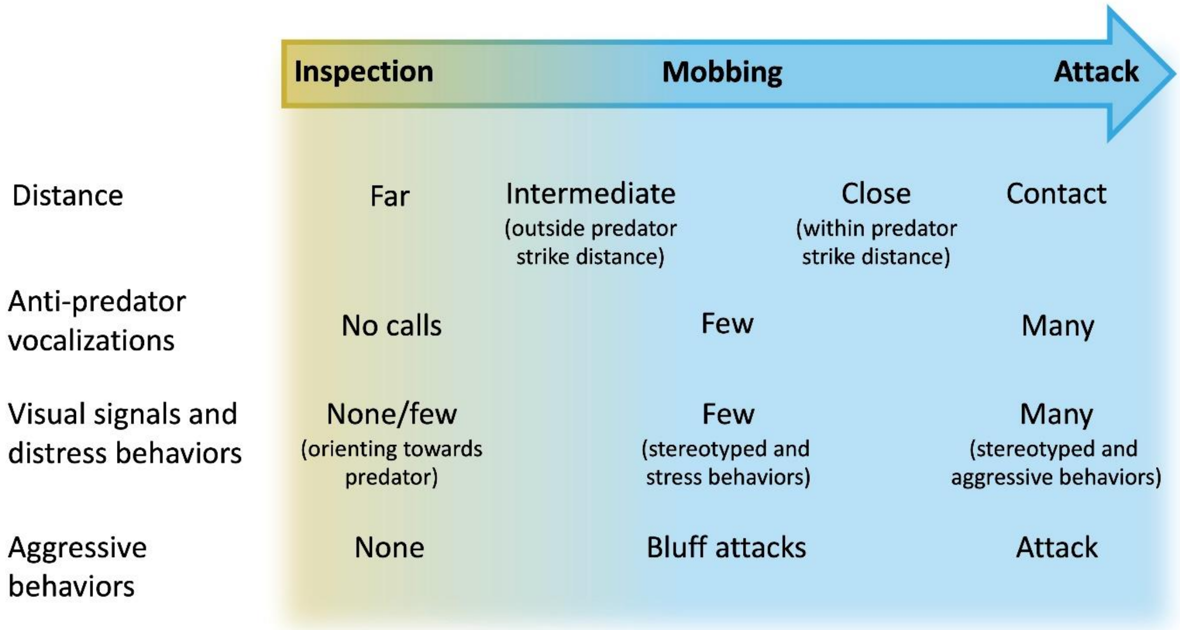

Figure 2: The progression from predator inspection to mobbing including aggressive attacks. Mobbing behavior is multidimensional and encompasses close physical distance, uttering many anti-predator vocalizations (only in vocal species), displaying diverse behaviors and visual signals, and aggression directed towards the predator.

1.2.2 What is not mobbing?

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 draw a clear line from, as it involves many of the same predator approach and stereotyped behaviors as mobbing (Figure 2). Moreover, predator inspection can serve a few similar functions as mobbing in some species (i.e., signaling to the predator it has been detected; Figure 3). However, unlike mobbing, predator inspection never includes harassment of the predator or physical contact, and while predator inspection can escalate into mobbing, the latter cannot deescalate into predator inspection (Figure 2, 3). Distress calls and flee/freeze calls are also anti-predator vocalizations used when encountering predators (Griesser, 2008; Magrath, Haff, & Igic, 2020; Marler, 1955, 1957, 1967). However, the conditions under which species give these calls and the responses they induce in others differ from mobbing. Distress calls are produced when an individual is already caught by a predator. These calls are thought to primarily serve to startle the predator into letting the prey go, though 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 calls similar to these can sometimes be heard during a mobbing event, they do not induce mobbing behavior. Finally, similar aggressive behavior where individuals harass and attack others to drive them away can occur between conspecifics and other non-predatory heterospecifics (e.g., noisy miners, *Manorina melanocephala,* Arnold, 2000; Dow, 1977). While many of the behaviors may look like mobbing, the threat to the mobber and the drive behind removing the intruder differ greatly.

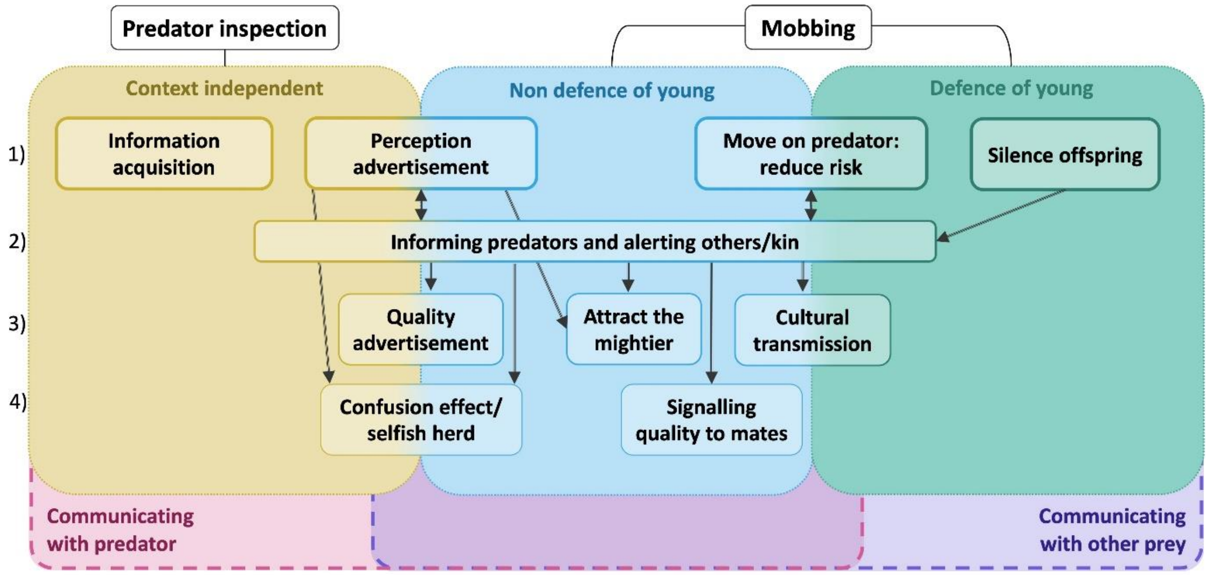

Figure 3: Links between predator inspection (left) and mobbing in non-defense of young (middle) and defense of young contexts (right), and the different functions of these behaviors. Primary functions are in the 1) top level, followed by 2) secondary, 3) tertiary, and 4) quaternary functions in descending 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, we have little idea of how risky this actually is. 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 be 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; many bird species, Sordahl, 1990; many primate species, Crofoot, 2012). However, given how infrequently this behavior is seen in the wild with live predators (e.g., five Siberian jay, *Perisoreus infaustus,* mobbing events observed during 2,300 field days, no individual was killed during these mobbing events, Griesser et al., 2017), it remains unknown how often mobbers are killed during a mobbing event. Similarly, there is little evidence regarding the cost of a mobber drawing attention to themselves with conspicuous signals (Krams, 2001), possibly increasing the chance of being singled out for an attack. Energetic costs are thought to be quite high (as this behavior is often quite vigorous in nature with increased movement and calling), though this aspect remains unexplored (Crofoot, 2012). Mobbing may also attract other predators. A few studies have shown that individuals that mob more intensely have increased nest predation rates (Krams, Krama, Igaune, & Mänd, 2007), while additional predators may be attracted to mobbing events (Fang, Hsu, Lin, & Yen, 2020; Smith, 1968). Finally, there are lost opportunity costs since a mobbing individual cannot engage in other behaviors including foraging or singing to attract a mate. These lost opportunity costs remain entirely unmeasured (Caro, 2005; Cresswell, 2008; Crofoot, 2012).

1.4 The ontogeny of mobbing

Mobbing behavior can either be an innate or learned behavior. Similar to other anti-predator behaviors, both modes can be observed even for different predators within the same species and can differ for the response to a predator and the response to mobbing behaviors of others. These differences can be based on whether or not young can experience predators without being in immediate danger (i.e., 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 nestlings will rapidly escape from the nesting cavity when they hear a mobbing call designating snakes which invade the cavities (Suzuki, 2011). After juveniles leave the safety of their home (den, burrow, nest, etc.) and can engage in mobbing behavior, there remain differences in evidence of innateness. In some species, naïve juveniles engage in mobbing behavior independent of whether more experienced individuals are present (e.g., California ground squirrels, *Spermophilus beecheyi*, and black-tailed prairie dogs, *Cynomys ludovicianus*, Owings & Coss, 1977; Owings & Owings, 1979), while in others, juveniles are not seen 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 difference may reflect that the costs of mobbing are higher for juveniles than older individuals as they are physically less capable and coordinated than adults. Alternatively, it may reflect that naïve juveniles 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 development of mobbing can provide important evidence for the evolution of mobbing, the ontogeny of mobbing and related anti-predator behavior remains understudied (but see: Hinde, 1954a, 1954b, 1961). Moreover, this process is more often studied in the lab than in the wild, while only in the latter individuals are exposed to predators in their natural environment.

1.5 Who is the recipient of mobbing calls?

Depending on the primary driver of mobbing, mobbing calls aim at conspecifics, the predator, and/or other predators. In birds, mobbing calls are thought to be designed as long-distance calls which travel through their habitats very well (Billings, 2018), and consequently, con- and heterospecifics can eavesdrop on these calls. Current research supports that eavesdropping is widely prevalent in communities with mobbing species, both within and between 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 some 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 increase anti-predator behavior such as bloating (skinks) and vigilance (iguanas) when they hear them. This prevalence of heterospecific eavesdropping is thought to create large anti-predator communication networks (Magrath et al., 2014) in communities of species 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. It is clear that mobbing serves an important ecological purpose in predator-prey dynamics, but this aspect remains less understood.

2. QUANTIFICATION OF MOBBING AND USE IN RESEARCH

For many researchers identifying mobbing behavior is not difficult but quantifying it has been more so. This difference likely reflects that mobbing can vary a lot both between and within lineages. While many studies provide descriptions of mobbing in their species, many more do not, or use only one specific behavior (often mobbing calls themselves) as a proxy for mobbing behavior.

2.1 How is mobbing measured?

Mobbing is often measured as either binary category (mobbing vs. not mobbing) or in degrees of intensity (e.g., approaching, approaching and calling, diving; e.g., Blancher & Robertson, 1982; Grim, 2007; Marzluff, DeLap, & Haycock, 2015; Owings, Coss, Mckernon, Rowe, & Arrowood, 2001; Table 2). Though different approaches to studying mobbing behavior, in both cases mobbing behavior itself needs to be quantified so it can be measured. Currently, mobbing is measured in six main ways in the literature, each with its own benefits and drawbacks.

Table 2. Table showing the six main ways mobbing behaviour 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, insects, 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 allows for 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

One of the most common methods of measuring mobbing (presence or intensity) is recording calling behavior of individuals engaging in mobbing. 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, making it a useful quantitative measure of mobbing. There are several metrics frequently used when examining mob calls, including calling behavior (e.g., number of individuals calling, Arnold, 2000; Coomes, McIvor, & Thornton, 2019; Królikowska, Szymkowiak, Laidlaw, & Kuczyński, 2016), gross measurements (e.g., 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 measurements of calls (e.g., call length, Courter, Perruci, McGinnis, & Rainieri, 2020; Ha et al., 2020; Kalb & Randler, 2019; peak frequency, Carlson, Greene, & Templeton, 2020; Furrer & Manser, 2009; Manser et al., 2014). While many studies have illuminated how different species encode information in their mobbing calls about threat, we still know very little about which individuals in a group call during mobbing events (i.e., do all individuals call, or just certain ones; but see (Francis et al., 1989; Gehlbach & Leverett, 1995; Griesser & Ekman, 2005; Griesser & Suzuki, 2016) and how much these calls actually reflect the caller's perceived level of threat vs. the predator's actual level of threat (but see: Carlson, Greene, et al., 2020). Determining whether a call is referential or influenced by the caller's perception of threat is more difficult to assess in species who use graded calls rather than species that use different calls for different classes or types of predators (Griesser, 2009; Suzuki, 2014).To determine if calling is a reflection of predator threat or perceived threat (i.e., the internal state of the caller) it is necessary to look at both calling and other mobbing behaviors/contexts. For example, some species increase calling rate along with other anti-predator behavior as a reflection of their internal state, while others modulate their call rate separately from other behaviours (Carlson, Greene, et al., 2020) increase mobbing call rate depending on the conspecific audience (e.g., presence of own offspring, Griesser & Ekman, 2005; presence of conspecific females, Cunha, Fontenelle, & Griesser, 2017b).

Another common method to measure presence and/or intensity of mobbing, is the closest distance prey approach the predator. Close approach can be telling in that one of the key aspects of mobbing is to harass and, in many cases, even attack the predator, which requires a close distance and the incurred risk in doing so. However, this distance can range from less than a meter ((Courter & Ritchison, 2010; Owings et al., 2001)) to 10 meters (Dutour, Lena, & Lengagne, 2017; Ficken & Popp, 1996) from the predator (Dutour et al., 2017; Ficken & Popp, 1996), and species will vary in what distance is relevant, often based on body size of the mobber and predator or the physical environment and availability of cover. Although approaching a predator is a key mobbing behavior, this does not allow us to separate mobbing from predator inspection, which has very different motivations, costs, and benefits than mobbing. Predator inspection, unlike mobbing, is primarily used by individuals to obtain information about a predator or potential predator, though it can also serve as a pursuit-deterrent signal (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. This does mean that approaches of a certain very close distance to a predator are almost always indicative of mobbing, though many studies use approaches at distances at which predator inspection and mobbing cannot be separated without other behaviors as well.

A third approach to measuring the presence and/or intensity of mobbing is measuring contact attacks (e.g., hitting, biting, etc.) or non-contact attacks (i.e., run/fly/swim by) towards the predator. Though not as common as other behaviors, attacking a predator is a clear diagnostic of mobbing behavior. If an individual attacks a predator, especially if the predator did not behave in a way to instigate an attack (i.e., killing/capturing a conspecific), then the attacking individual is definitely mobbing. While attacks are a clear identifier of mobbing behavior, not all mobbing events escalate to include attacking, 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 species.

A fourth approach uses levels of activity as a measure for the presence and/or intensity of mobbing including calling rate (Courter & Ritchison, 2012; Cross & Rogers, 2006; Dutour, Kalb, Salis, & Randler, 2021), approach rate/proportion (Andersen, 1990; Dutour, Cordonnier, Lena, & Lengagne, 2019), number of individuals/species participating/arriving (Arnold, 2000; Clode et al., 2000), duration within close proximity to predator (Feeney & Langmore, 2013; Owings et al., 2001). While increased mobbing activity is a good way to capture the intensity of mobbing behavior, this proxy can be vague and difficult to quantify and keep consistent across species or studies.

A 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 individuals involved cannot miss the onset of a signal (i.e., all measured individuals are in direct sight line or hearing distance) it can be difficult to determine whether a latency to respond or non-response is due to a lack of response or a lack of reception of 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 more comprehensive and accurate way to measure mobbing behavior, many of these scales still include vague or species-specific subjective measures that differ hugely across studies making comparative research difficult.

Finally, though not actually a way to *measure* mobbing, per se, many observational studies and natural history reports will include detailed and comprehensive descriptions of mobbing in the target species (even if they do not use this to measure mobbing behavior). Many of the papers that include detailed descriptions of mobbing behavior are natural history reports or observations which do not attempt to answer any questions, but simply describe the behavior (Deng, Lee, & Wee, 2008; Hein, 1996; Passamani, 1995). Other papers, however, provide theories (tested or not) about the origins, development, or motivations of the observed behavior with detailed descriptions (Clemmons & Lambrechts, 1992; Curio & Regelmann, 1985; Ishihara, 1987; Owings & Coss, 1977). These papers also tend to draw clear parallels between the described species and other species putting them in a larger mobbing behavior context.

2.2 Can and should we measure mobbing intensity?

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

Different lineages have a different body design, and thus, mobbing is expressed differently across different lineages. For example, mammals have lineage specific mobbing characteristics including ear, tail, and fur postures that are indicative of mobbing (Berger, 1979; Graw & Manser, 2007; Owings & Loughry, 1985; Owings & Owings, 1979) (and throwing of objects/substrate in some species e.g., 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 insects sting and heat-ball (Ono, Igarashi, Ohno, & Sasaki, 1995; Seeley et al., 1982); though not called mobbing, swarming a predator fits most definitions. Even within taxonomic lineages (e.g., Mammalia), species with different gross morphology can display different mobbing behaviors. Primates for example, often use their arms and even sticks etc. to threaten or attack a predator (Boinski, 1988), where 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). 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'. In many bird species the degree of cover may impact how close individuals get to a predator; if there is good safe cover all around the predator for the mobbing individual to escape into, they may be more willing to approach more closely than if the predator is very exposed with no dense cover nearby (N.C. and M.G. per obs.). Similarly, lower threat situations (i.e., more 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 individuals who are bolder (e.g., more neophilic) are often more aggressive mobbers (Vrublevska et al., 2014) and differences in average aggressiveness across different populations could result in very different mobbing responses (Davies & Sewall, 2016; Hardman & Dalesman, 2018) . While measuring mobbing intensity provides useful information about the selective pressures, risk, and perception of mobbing species, there needs to be a detailed and standardized approach to describing and reporting mobbing behavior across species and studies for it to be widely applicable.

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

While mobbing is incredibly prevalent across the animal kingdom, our ability to compare mobbing behavior across species is limited due to differences in measurement and approaches to studying mobbing. Currently, much of the comparative research focuses on specific communities or specific lineages, trying to understand commonalities among species to elucidate evolutionary pressures that facilitate mobbing behavior (Carlson, Healy, et al., 2017b; Crofoot, 2012; Cunha, Fontenelle, & Griesser, 2017a; Gottfried, 1979; Hua & Sieving, 2016; Manser et al., 2014).

Research focusing on specific communities provides useful insights to mobbing prevalence and species characteristics among those communities, however, many of these studies are restricted in their conclusions due to a several factors. First, most of these studies do not clearly differentiate between a mobbing response and predator inspection (e.g., an individual is counted as mobbing if it approached within 10 m, Dutour et al., 2017; Ficken & Popp, 1996), creating ambiguity as to whether an individual is engaging in predator inspection or mobbing. Second, while several studies do consider multiple sources of variation, few addressed enough of these possible sources of variation to thoroughly interrogate the entire system. This shortcoming inflates 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 that species mobs (e.g., the type of predator used, time of year, degree of cover). For example, many studies only conduct experiments during one season (excluding any species who only mob 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), or with one type or size of predator (Lima et al., 2018; Pawlak et al., 2019). As predators are only a risk for some species but not others (Cunha et al., 2017a), this limits a predator’s likelihood to elicit a mobbing response from certain species and increases the chance they are classified as non-mobbers.

Research focusing on specific lineages also provide useful insights into specific traits that may facilitate mobbing behavior or explores the variation of mobbing behavior in similar species while controlling for phylogeny. However, these studies tend to be too narrowly focused, 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). These lineage-focused comparative studies often fail to examine the breadth of similar species within a lineage (e.g., the Paridae family), or to specifically include non-mobbing species to better understand how mobbing may have evolved in the target lineage. This lack of breadth limits the conclusions drawn about mobbing to the few species within the lineage studied.

While these studies do generate important data, we need to understand which species mob and to what degree, which species eavesdrop but do not mob, and which species do not engage in mobbing events in any way, as well as how mobbing is expressed across a wide range of species within lineages. Only by having these details will we be able to unravel the evolutionary pressures and current ecological conditions that result in mobbing behavior being expressed across species, taxa, and environments.

3. WHAT IS THE FUNCTION OF MOBBING?

Mobbing and its function (i.e., how does this behavior benefit individuals that engage in it) remain in contention in the literature. Curio proposed ten hypotheses as to the purpose of mobbing (Curio, 1978), and continued research has shown that the function of mobbing is likely a combination of more than one of these hypotheses (Figure 3). Additionally, due to their inherent interconnectedness, multiple hypotheses often are inseparable from one another or provide similar outcomes (i.e., different motivations for mobbing result in the same beneficial outcome; Figure 4). These hypotheses can be broken down into three main general benefits/categories of how they help a mobbing individual: physically remove the predator, disrupt the predator hunting behavior, and communicating with other potential prey.

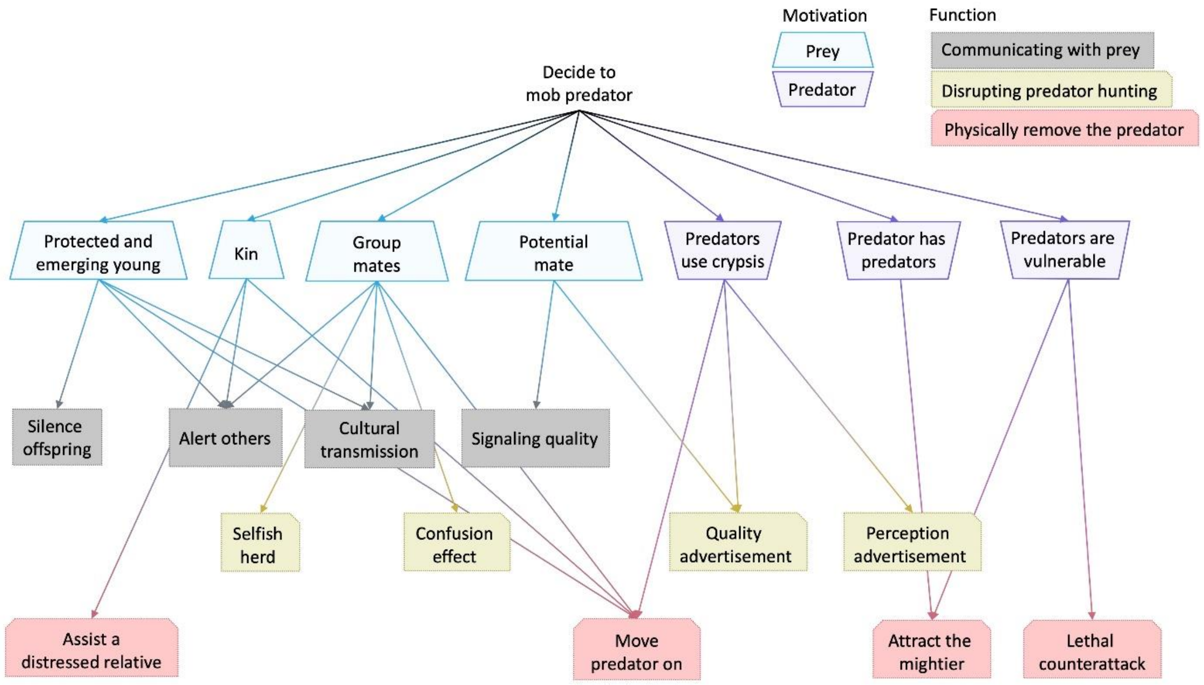

Figure 4: The interconnections of the motivations and functions of mobbing based on Curio's ten mobbing hypotheses. When deciding to mob, individuals can have one or more different motivations concerning other prey or the predator, which in turn can serve a number of different functions with similar outcomes.

<u>3.1 Curio's ten hypotheses</u>

3.1.1 Physically remove the predator

There are a few hypotheses that focus on how mobbing can effectively remove the predator from the area, either through moving-on, injury, or death.

The 'move on' hypothesis

The move on hypothesis stipulates that mobbing behavior will cause a predator to change movement patterns (Bildstein, 1982), leave the area sooner (Clark, 2005), fly farther away (Pettifor, 1990), and maybe even avoid the 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 though few studies have been done from the point of view of the predators themselves. The studies that have looked at predator response to mobbing show a lower presence of mobbing species in the predator's diet (Ekman, 1986; Pavey & Smyth, 1998), avoidance of areas containing mobbing prey by predators for roosting (Pavey & Smyth, 1998), altering special use

(Bildstein, 1982; Clark, 2005; Pettifor, 1990), and increased agitation by predators being mobbed, especially by larger prey (Consla & Mumme, 2012; Curio & Regelmann, 1985).

Attract the mightier

The *attract the mightier hypothesis* stipulates that mobbing behavior and/or calls of the prey species will attract a different predator to the mobbing area that preys on the predator species currently being mobbed, thus removing the threat (Grim, 2007). Three studies have examined this hypothesis (Fang et al., 2020; Grim, 2007; Gursky, 2006), though only one showed some support for it (Fang et al., 2020).

Lethal counterattack

The *lethal counterattack hypothesis* stipulates that the act of mobbing will kill the predator, thus removing the threat. While not especially common and almost entirely untested experimentally (but see: Lourenço, Penteriani, Delgado, Marchi-Bartolozzi, & Rabaça, 2011), there are multiple field observations of prey mobbing and killing their predators including in primates (Crofoot, 2012), honeybees (Ono et al., 1995), raptors (Lourenço et al., 2011), fasciated antshrikes, *Cymbilaimus lineatus* (Chiver, Jaramillo, & Morton, 2017).

3.1.2 Disrupting predator hunting strategy/advantage

The 'selfish herd' & 'confusion effect' hypotheses

The selfish herd and confusion effect hypothesis stipulate 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; 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 there are, the lower chance any one individual is eaten). In the *confusion effect hypothesis* this is achieved by affecting the predator's ability to target one individual (i.e., many individuals moving rapidly near each other makes it harder for the predator to focus on one individual). Support for these hypotheses are difficult to tease apart, but 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 stipulates that the mobbing signals themselves make the predator give up on hunting prey, by signaling that the predator will have low or no success should they try (Caro, 2005; Frankenberg, 1981; Smythe, 1970). In the *perception advertisement hypothesis*, the prey signals the predator 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/agility means that they can outrun/escape from the predator 's potential attack. Clark (2005) showed that the mobbing of timber rattlesnakes (*Crotalus horridus*) by a number of its prey species (chipmunks, *Tamias striatus*; eastern gray squirrels, *Sciurus carolinensis)* was a pursuit deterrent signal as the snakes only moved on faster if they were actively hunting rather than basking (Clark, 2005). While few studies have examined mobbing in this specific context (though see: Clark, 2005; Gursky, 2006), many predator inspection experiments have shown that when engaging in behavior that signals to the predator it has been detected (e.g., orienting toward the predator, Frankenberg, 1981), or that the prey are agile enough to escape them (e.g., stotting in Thomson's gazelles, *Gazella thomsoni,* FitzGibbon & Fanshawe, 1988; singing in skylarks, *Alauda arvensis,* Cresswell, 1994) many predators will give up.

Aiding a distressed relative

The *aiding a distressed relative hypothesis* is only applicable when an individual is already caught by a predator. It stipulates that mobbing the predator who has caught a relative or group member, will distract the predator so that the caught individual can escape. While few studies have explicitly studied this hypothesis itself, predator mounts with 'captured' prey (both dead and alive) are not uncommon as a method to elicit mobbing behavior in others (Barash, 1976; Carlson, Pargeter, & Templeton, 2017; Chu, 2001); often these mobbing events are thought to be more intense and, when coupled with dead conspecifics, have stronger lasting power in the prey species (Barash, 1976; Conover & Perito, 1981). Additionally, while rare, field observations have documented individuals mobbing predators when they have caught prey (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 stipulate that mobbing produces a signal or information that upon receipt increases a receiver's chance of survival.

Alerting others hypothesis

The *alerting others hypothesis* stipulates that mobbing signals the danger to others in the vicinity, allowing them to take appropriate action before they have seen the predator and thereby increasing their chance of survival (Carlson, Healy, & Templeton, 2018; Colombelli-Négrel, Robertson, & Kleindorfer, 2010; Suzuki, 2011, 2015). Evidence for this hypothesis shows that individuals are more likely to mob a predator when 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, & Igaune, 2006; Krams, Krama, & Iguaune, 2006) are present. Receivers frequently respond to mobbing calls with increased alert behaviour/posture, which could increase survival if a predator were to attack (Dutour & Danel, 2020; Graw & Manser, 2007; Ito & Mori, 2010). While some evidence shows that individuals may be communicating to other 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). There is evidence, however, that 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 be a driving factor in 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 stipulates that by mobbing, a parent will decrease their offspring's' risk of being depredated by inducing a beneficial change in their behaviour. For example, nestlings of many bird species will become quiet (e.g., Eastern bluebirds, *Sialia sialis,* Grabarczyk & Ritchison, 2015; and red-winged blackbirds, *Agelaius phoeniceus,* Knight & Temple, 1988), crouch down (e.g., Japanese tit, *Parus minor;* Ha et al., 2020; Suzuki, 2011) and Eastern bluebirds

(Grabarczyk & Ritchison, 2015)), force fledge (e.g., Japanese tits (Ha et al., 2020; Suzuki, 2011)), or engage in other anti-predator behaviours that reduce their risk of being eaten when they hear their parents' mobbing calls, even if they have never seen the predator (e.g., Japanese tits; Ha et al., 2020; Suzuki, 2011). In many species, these behavioural responses to parents' mobbing calls change as the young develop, and different responses are more beneficial (Hinde, 1954a, 1954b, 1961; Suzuki, 2011), and parents 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 stipulates that by observing mobbing, naïve individuals will learn something about either the predator itself or the place it often occurs, which will allow them to avoid the predator or place in the future. There is support in the literature for this hypothesis as many species appear to be able 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 the main predator (goshawk, *Accipiter gentilis*) had a better overwinter survival than those that did not, suggesting that they learned to avoid goshawks (Griesser & Suzuki, 2017). However, cultural transmission of predator threat information does vary across species and has yet to be either tested in relation to learning about dangerous places, however there is evidence that suggests that in some cases, with immobile predators, individuals will avoid that predator's location after mobbing. For example Peters' monocle bream, *Scolopsis affinis*, will avoid foraging near a Bobbit worm, *Eunice aphroditois*, once it has been discovered and mobbed (Lachat & Haag-Wackernagel, 2016).

3.1.4 Other non-Curio hypothesis

Signaling quality to potential breeding partners

The *sexual signaling hypothesis* provides a non-antipredator focused function of mobbing behavior. It stipulates that an individual can indirectly show off their quality (e.g., mobility, boldness, etc.) by putting themselves in danger during mobbing while successfully avoiding being eaten (Zahavi, 1977). While a few studies have tried to test this hypothesis (e.g., Cunha et al., 2017b; Maklakov, 2002), there remains mixed predictions and support. One study showed support for this hypothesis with their finding that males increase their mobbing intensity in the presence of conspecific females, particularly when mobbing a more dangerous predator (Cunha et al., 2017b). However, this study did not follow up by examining if bolder or more frequent mobbers father more chicks or are in better condition than others (Cunha et al., 2017b).

Mobbing mimicry

Multiple species have been reported mimicking heterospecific mobbing calls. There are many different hypotheses in these species to explain why this may occur. Thick-billed euphonias, *Euphonia laniirostris*, mimicked the alarm call of a yellow-green vireo, *Vireo flavovirids*, causing neighboring vireos mobbing the 'predator' Morton 1976 in (Chu, 2001). 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). Greater racket-tailed drongos, *Dicrurus paradiseus*, mimic mixed-species flock mobbing events to draw the flocks to them so they can join the flock (Goodale, Ratnayake, & Kotagama, 2014). In Superb lyrebirds, *Menura novaehollandiae*, males effectively mimic multi-species mobbing events and it is thought to prevent females from leaving a display area or to prolong mating to ensure a better chance of success (Dalziell, Maisey, Magrath, & Welbergen, 2021).

3.2 Links among Curio's hypotheses and potential evolutionary drivers for mobbing

While many theories about the specific purpose of mobbing are detailed in the literature, little research has focused on what pressures/selective forces gave rise to this behavior. While all ten of Curio's hypothesis explain why an individual may mob, some functions are likely to be primary functions, and therefore a driver behind the evolution of this behavior, while others may be secondary or tertiary functions that were more likely to have arisen after mobbing was an established anti-predator behavior (Figure 3). To examine these links, it is important to differentiate between evolutionary drivers that gave rise to mobbing and the social and ecological conditions that maintain it in both the context of young defense (i.e., mobbing in any protected area where adults raise young – e.g., nest, burrow, den) and non-young defense as they likely had different evolutionary pressures.

When examining young defense mobbing, both silencing offspring and removing the predator (to reduce the potential risk incurring to offspring) are likely primary functions. In birds, begging calls are a conspicuous signal that can draw attention to the nest, and provisioning is thought to partially be a way to silence these conspicuous signals (Magrath, Haff, Horn, & Leonard, 2010; McDonald, Wilson, & Evans, 2009). Quieter nests (i.e., ones where adults silenced offspring) are more likely to fledge more offspring as they are less likely to be discovered by a nest predator (McDonald et al., 2009). When encountering predators near the nest or den, many species have a variety of anti-predator defense behaviors including mimicking a dangerous animal (hissing), leading a predator away (distraction display), and attacking the predator (mobbing; (Caro, 2005)). These types of harassment may have arisen as part of a suite of different nest defense behaviors and increased aggression towards intruders, specifically predators. In both young defense strategies, parents are communicating either with their offspring, or with their mate and/or the predator itself. This communication about a predator could eventually lead to cultural transmission about predator threat if sufficient information to differentiate between threats is contained in the mobbing signal/behavior (Figure 3).

For non-young defense mobbing, predator inspection is a likely precursor. Though different, there are many similarities in mobbing and predator inspection (Figure 2), and predator inspection can escalate into mobbing (though 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 as a motivation is likely different between both behaviors. In predator inspection, information acquisition is thought to be 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 likely a secondary or negligible motivation for mobbing. Perception advertisement is likely shared between mobbing and predator inspection, as both behaviors always (mobbing) or often (predator inspection) 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). Like with young defense mobbing, removing the predator is likely a primary function of mobbing in non-young defense contexts. In both contexts, however, mobbers are signaling to multiple receivers (the predator, conspecifics, heterospecifics) meaning that alerting/informing others may be a primary or close secondary function of mobbing. This communication with others (including the predator) lends itself to other functions such as attracting the mightier, cultural transmission, advertising the mobber’s quality to the predator (quality advertisement) or to conspecifics (sexual signaling) and can lead to recruitment of others to reduce risk through the confusion or selfish herd effects (Figure 4). 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 lineages to achieve a broader picture.

3.3 Mobbing motivation and behavioral outcomes

When examining a mobbing event from detecting the predator, through information acquisition, to deciding to mob (Figure 1), there are many sources of motivation that could result in mobbing (Figure 4). Discerning the primary motivation for mobbing can be difficult as in most cases mobbing is driven by a number of different factors based on both prey and predator life history and ecology. Additionally, the desired outcomes of mobbing may be diverse and/or numerous (i.e., one or more of: removing the predator, disrupting predator hunting, communicating with prey species; Figure 4). This conundrum creates a problem for researchers when trying to understand the driving motivations and desired outcomes that result in an individual mobbing in any given circumstance.

4. MOBBING AS A PROXY FOR ‘COGNITION’

While mobbing is a fascinating anti-predator behavior on its own, a large portion of the studies that measure some aspect of mobbing behavior (69%; Table 1), do not focus on the behavior itself, but rather use the mobbing response as a proxy to understand cognitive processes in three major areas: predator recognition/categorization, information encoding/language-like adaptations, and learning (e.g., social, experiential).

Mobbing is a useful tool to study predator recognition and categorization, as it is a graded behavioral response that differs among predator types, threats, etc. allowing for straightforward experiments that ask the responding individual how *they* perceive the predator. Many studies have been able to determine to what degree 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 even what 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; N. B. Davies &

Welbergen, 2009; Němec et al., 2014; Trnka, Prokop, & Grim, 2012). Mobbing calls are also often used to determine the perception of caller reliability (i.e., is the caller reliable in 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 is a very 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 often 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). Many studies have been able to determine what types of 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) by experimentally manipulating the perceived threat and type of different predators and situations.

Finally, mobbing is also an interesting tool to study learning. Though the stereotyped behavior and calls exhibited during mobbing may (or may not) be innate, many species have shown that the association between mobbing behavior and a predator threat may be 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, many studies have examined the degree to which individuals can learn to recognize new predators or new mobbing calls by being exposed to the new stimulus alongside a simulated mobbing event (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).

These studies provide insights into perception, language-like adaptations, and learning. However, we still lack an understanding of many fundamental aspects of mobbing including i) the ecological conditions that produced and maintain this behavior, ii) the sources of variation (outside predator thereat) in this behavior, and iii) the prevalence of this behavior. Additionally, many studies that include mobbing, focus on only one aspect of this behavior (e.g., mobbing calls). Some studies, for example, have already shown that vocal and behavioral measures of mobbing may differ based on the source of the information (Carlson, Greene, et al., 2020), which could impact studies examining information encoding or predator recognition because many species will respond differently based on the reliability of even a specific caller within a group (Cheney & Seyfarth, 1988; Silvestri, Morgan, & Ridley, 2019). Other studies show that learner state can have a substantial impact on learning (Griffin, 2004), suggesting that when examining learning, a lack of learning may not indicate that a species cannot learn through mobbing, rather that the conditions for learning may have not been met. While mobbing is a very useful tool for studying the above questions and has been employed successfully, a better understanding and quantification of the behavior itself, will help to create stronger more robust base from which to continue asking more targeted and detailed questions.

5. CONCLUSIONS AND MOVING FORWARD

Moving forward we should approach mobbing in a more standardized way to allow for comparative work, and we identify four major areas of research that need further investigation: factors that influence mobbing behavior (aside from threat), taxonomic bias, cost benefit explorations, and responses to anthropogenic changes.

5.1 Standardization and quantification of mobbing

There is a need for a clear and consistent use of an inclusive mobbing definition that accounts for differences in mobbing behavior across taxa, but still remains specific enough to rule out behaviors with different motivations, costs, and benefits, like predator inspection. 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 defence strategies (e.g., distraction displays). By including conspicuous, stereotyped movements and/***or*** vocalizations, we allow for definitions that 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 lineages, the evolutionary drivers that gave rise to mobbing behavior, and the ecological conditions that maintain it. In light of this, we have 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 Figures 1-3) studies moving forward remove much of the subjectivity that limits comparative studies and allows for a better understanding of what exactly constitutes mobbing behavior across all studies that examine it.

5.2 Areas requiring further investigation

We identify four major areas of mobbing that remain in need of more targeted examination to better understand the evolutionary drivers that gave rise to mobbing and the social and ecological conditions that maintain it: i) the factors that influence mobbing behavior (aside from threat), ii) defining the costs and benefits associated with mobbing, iii) overcoming taxonomic bias, and iv) the possible effects of anthropogenic change.

5.2.1 Other factors effecting mobbing

While it is difficult to control for all factors that may influence mobbing in the same study, it is important to understand how non-predator sources of variation affect mobbing. We therefore highlight that studies would need to examine the differences that season (e.g., breeding and non-breeding seasons) has on mobbing behavior, how the predators presented influence the species present, how ecological factors such as degree of close cover or habitat type, the perceived predation pressure, and the presence of other individuals (e.g., females, juveniles, heterospecifics) impacts mobbing behavior. Understanding the effects of these factors on mobbing behavior and propensity will enable us to understand the evolutionary drivers that gave rise to mobbing and the social and ecological conditions that maintain it.

5.2.2 Costs and benefits

The costs and benefits of mobbing are another area that can shed more light on its ecological and evolutionary pressures. Few studies have examined the costs and benefits of mobbing and most focus on other aspects 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). Overcoming this current bias will allow us to determine the actual ubiquity of mobbing across the animal kingdom, and will shed light on its facilitators, the ancestral state within lineages and the evolutionary transitions across species.

5.2.4 Mobbing and anthropogenic change

Finally, as the impact of human activities on animal behavior, communication, and conservation is becoming more and more clear, there is a need to address the effects of anthropogenic change on mobbing behavior. Currently there are only a few studies addressing the effects of anthropogenic change on mobbing and the majority of those focus on signal reception (i.e., does anthropogenic noise mask anti-predator calls; (Grade & Sieving, 2016; Templeton, Zollinger, & Brumm, 2016)). Human impacts, however, have further changes on both population composition, habitat structure (i.e., urbanization gradients), noise, chemical, and light pollution, and climate change. To minimize the far-reaching impacts of global anthropogenic change, we need to understand how all of the above factors may impact mobbing behavior, the information carried through anti-predator communication networks, and the participants in these events.

5.3 Summary and overall conclusions

Mobbing is an important anti-predator strategy used by an astounding number of species across lineages. However, for all its prevalence and importance, the behavior (excluding vocalizations) remains largely understudied. By creating a more inclusive and standardized definition and documenting scheme, and turning our attention to understudied areas, 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.

ACKNOWLEDGEMENTS

We thank Toshitaka Suzuki and Christopher N Templeton for general discussions on the topic. MG was supported by Heisenberg Grant nr. GR 4650/2-1 of the German Research Foundation DFG.

REFERENCES

Altmann, S. A. (1956). Avian mobbing behavior and predator recognition. *Condor*, *58*(4), 241–253.

Andersen, D. E. (1990). Nest-defense behavior of red-tailed hawks. *Condor*, *92*(4), 991–997.

Aristotle. (350AD). *The History of Animals*. (D. W. Thompson, Tran.).

Arnold, K. E. (2000). Group mobbing behaviour and nest defence in a cooperatively breeding Australian bird. *Ethology*, *106*, 385–393.

Baker, M. C. (2004). Socially learned antipredator behaviour in black-capped chickadees (*Poecile atricapillus*). *Bird Behavior*, *16*, 13–19.

Baker, M. C., & Becker, A. M. (2002). Mobbing calls of black-capped chickadees: effects of urgency on call production. *The Wilson Bulletin*, *114*(4), 510–516.

Bakker, J., & Langermans, J. A. M. (2018). Chapter 49 Ultrasonic components of vocalizations in marmosets. In S. M. Brudzynski (Ed.), *Handbook of Ultrasonic Vocalization, A Window into the Emotional Brain*, Handbook of Behavioral Neuroscience (Vol. 25, pp. 535–544). Elsevier.

Barash, D. P. (1976). Mobbing behavior by crows: the effect of the "crow-in-distress" model. *Condor*, *78*(1), 120.

Bartmess-LeVasseur, J., Branch, C. L., Browning, S. A., Owens, J. L., & Freeberg, T. M. (2010). Predator stimuli and calling behavior of Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*). *Behavioral Ecology and Sociobiology*, *64*(7), 1187–1198.

Beránková, J., Veselý, P., & Fuchs, R. (2015). The role of body size in predator recognition by untrained birds. *Behavioural Processes*, *120*, 128–134.

Beránková, J., Veselý, P., Sýkorová, J., & Fuchs, R. (2014). The role of key features in predator recognition by untrained birds. *Animal Cognition*, *17*(4), 963–971.

Berger, J. (1979). " Predator Harassment" as a Defensive Strategy in Ungulates. *The American Midland Naturalist*, *102*(1), 197.

Bildstein, K. L. (1982). Responses of Northern harriers to mobbing passerines. *Journal of Field Ornithology*, *53*(1), 7–14.

Billings, A. C. (2018). The low-frequency acoustic structure of mobbing calls differs across habitat types in three passerine families. *Animal Behaviour*, *138*, 39–49.

Blancher, P. J., & Robertson, R. J. (1982). Kingbird aggression: does it deter predation? *Animal Behaviour*, *30*(3), 929–930.

Boinski, S. (1988). Use of a club by a wild white-faced capuchin (*Cebus capucinus*) to attack a venomous snake (*Bothrops asper*). *American Journal of Primatology,* (14), 177–179.

Branch, C. L., & Freeberg, T. M. (2012). Distress calls in tufted titmice (*Baeolophus bicolor*): are conspecifics or predators the target? *Behavioral Ecology*, *23*(4), 854–862.

Brudzynski, S. M. (Ed.). (2018). *Handbook of Ultrasonic Vocalization - A Window into the Emotional Brain*. Elsevier. Elsevier.

Buitron, D. (1983). Variability in the responses of black-billed magpies to natural predators. *Behaviour, 87*(3–4), 209–235.

Campbell, M. W., & Snowdon, C. T. (2007). Vocal response of captive-reared *Saguinus oedipus* during mobbing. *International Journal of Primatology*, *28*(2), 257–270.

Carlson, N. V., Greene, E., & Templeton, C. N. (2020). Nuthatches vary their alarm calls based upon the source of the eavesdropped signals. *Nature Communications*, *11*, 526.

Carlson, N. V., Healy, S. D., & Templeton, C. N. (2017a). Hoo are you? Tits do not respond to novel predators as threats. *Animal Behaviour*, *128*, 79–84.

Carlson, N. V., Healy, S. D., & Templeton, C. N. (2017b). A comparative study of how British tits encode predator threat in their mobbing calls. *Animal Behaviour, 125*, 77–92.

Carlson, N. V., Healy, S. D., & Templeton, C. N. (2018). Mobbing. *Current Biology*, *28*(18), R1081–R1082.

Carlson, N. V., Healy, S. D., & Templeton, C. N. (2019). Wild fledgling tits do not mob in response to conspecific or heterospecific mobbing calls. *Ibis*, *162*(3), 1024–1032.

Carlson, N. V., Healy, S. D., & Templeton, C. N. (2020). What makes a “community informant?” Reliability and anti-predator signal eavesdropping across mixed-species flocks of tits. *Animal Behavior and Cognition*, *7*(2), 214–246.

Carlson, N. V., Pargeter, H. M., & Templeton, C. N. (2017). Sparrowhawk movement, calling, and presence of dead conspecifics differentially impact blue tit (*Cyanistes caeruleus*) vocal and behavioral mobbing responses. *Behavioral Ecology and Sociobiology*, *71*(9), 437–11.

Caro, T. (2005). *Antipredator Defenses in Birds and Mammals*. University of Chicago Press. University of Chicago Press.

Cheney, D. L., & Seyfarth, R. M. (1988). Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, *36*, 477–487.

Chiver, I., Jaramillo, C. A., & Morton, E. S. (2017). Mobbing behavior and fatal attacks on snakes by fasciated antshrikes (*Cymbilaimus lineatus*). *Journal of Ornithology, 158*(4), 935–942.

Chu, M. (2001). Heterospecific responses to scream calls and vocal mimicry by phainopeplas (*Phainopepla nitens*) in distress. *Behaviour, 138*(6), 775–787.

Clark, R. W. (2005). Pursuit-deterrent communication between prey animals and timber rattlesnakes (*Crotalus horridus*): the response of snakes to harassment displays. *Behavioral Ecology and Sociobiology, 59*(2), 258–261.

Clemmons, J. R., & Lambrechts, M. M. (1992). The waving display and other nest site anti-predator behavior of the black-capped chickadee. *The Wilson Bulletin, 104*(4), 749–756.

Clode, D., Birks, J. D. S., & Macdonald, D. W. (2000). The influence of risk and vulnerability on predator mobbing by terns (*Sterna spp.)* and gulls (*Larus spp.*). *The Zoological Society of London, 252*, 53–59.

Clucas, B. A., Freeberg, T. M., & Lucas, J. R. (2004). Chick-a-dee call syntax, social context, and season affect vocal responses of Carolina chickadees (*Poecile carolinensis*). *Behavioral Ecology and Sociobiology, 57*(2), 187–196.

Colombelli-Négrel, D., Robertson, J., & Kleindorfer, S. (2010). Nestling presence affects the anti-predator response of adult superb fairy-wrens (*Malurus cyaneus*). *Acta Ethologica, 13*(2), 69–74.

Conover, M. R. (1987). Acquisition of predator information by active and passive mobbers in ring-billed gull colonies. *Behaviour, 102*(1/2), 41–57.

Conover, M. R., & Perito, J. J. (1981). Response of starlings to distress calls and predator models holding conspecific prey. *Zeitschrift für Tierpsychologie - Journal of Comparative Ethology, 57*, 163–172.

Consla, D. J., & Mumme, R. L. (2012). Response of captive raptors to avian mobbing calls: the roles of mobber size and raptor experience. *Ethology, 118*(11), 1063–1071.

Coomes, J. R., McIvor, G. E., & Thornton, A. (2019). Evidence for individual discrimination and numerical assessment in collective antipredator behaviour in wild jackdaws (*Corvus monedula*). *Biology Letters, 15*(10), 20190380–6.

Coppinger, B. A., Kania, S. A., Lucas, J. R., Sieving, K. E., & Freeberg, T. M. (2020). Experimental manipulation of mixed-species flocks reveals heterospecific audience effects on calling. *Animal Behaviour, 167*, 193–207.

Corrêa, H. K. M., & Coutinho, P. E. G. (1997). Fatal attack of a pit viper, *Bothrops jararaca*, on an infant buffy-tufted ear marmoset (*Callithrix aurita*). *Primates, 38*(2), 215–217.

Courter, J. R., Perruci, R. J., McGinnis, K. J., & Rainieri, J. K. (2020). Black-capped chickadees (*Poecile atricapillus*) alter alarm call duration and peak frequency in response to traffic noise. *PLoS ONE, 15*(10), e0241035-10.

Courter, J. R., & Ritchison, G. (2010). Alarm calls of tufted titmice convey information about predator size and threat. *Behavioral Ecology, 21*(5), 936–942.

Courter, J. R., & Ritchison, G. (2012). Asymmetries in mobbing behavior among nuclear flcokmates. *The Wilson Journal of Ornithology*, *124*(3), 626–629.

Cresswell, W. (1994). Song as a pursuit-deterrent signal, and its occurrence relative to other anti-predation behaviours of skylark (*Alauda arvensis*) on attack by merlins (*Falco columbarius*). *Behavioral Ecology and Sociobiology*, *34*(3), 217–223.

Cresswell, W. (2008). Non-lethal effects of predation in birds. *Ibis*, *150*, 3–17.

Crofoot, M. C. (2012). Why mob? Reassessing the costs and benefits of primate predator harassment. *Folia primatologica*, *83*(3–6), 252–273.

Cross, N., & Rogers, L. J. (2006). Mobbing vocalizations as a coping response in the common marmoset. *Hormones and Behavior*, *49*(2), 237–245.

Cully, J. F., & Ligon, J. D. (1986). Seasonality of mobbing intensity in the pinyon jay. *Ethology*, *71*(4), 333–339.

Cunha, F. C., & Griesser, M. (2021). Who do you trust? Wild birds use social knowledge to avoid being deceived. *Science Advances*, 1–19.

Cunha, F. C. R., Fontenelle, J. C. R., & Griesser, M. (2017). Predation risk drives the expression of mobbing across bird species. *Behavioral Ecology*, *28*(6), 1517–1523.

Cunha, F. C. R., Fontenelle, J. C. R., & Griesser, M. (2017). The presence of conspecific females influences male-mobbing behavior. *Behavioral Ecology and Sociobiology*, *71*, 52.

Curio, E. (1975). The functional organization of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. *Animal Behaviour*, *23*, 1–115.

Curio, E. (1978). The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. *Zeitschrift für Tierpsychologie - Journal of Comparative Ethology*, *48*, 175–183.

Curio, E., Ernst, U., & Vieth, W. (1978a). The adaptive significance of avian mobbing. II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints. *Zeitschrift für Tierpsychologie - Journal of Comparative Ethology*, *48*, 184–202.

Curio, E., Ernst, U., & Vieth, W. (1978b). Cultural transmission of enemy recognition: one function of mobbing. *Science, New Series*, *202*(4370), 899–901.

Curio, E., & Regelmann, K. (1985). The behavioural dynamics of great tits (*Parus major*) approaching a predator. *Zeitschrift für Tierpsychologie - Journal of Comparative Ethology*, *69*(1), 3–18.

Dalziell, A. H., Maisey, A. C., Magrath, R. D., & Welbergen, J. A. (2021). Male lyrebirds create a complex acoustic illusion of a mobbing flock during courtship and copulation. *Current Biology*, *31*, 1–7.

Davies, N. B., & Welbergen, J. A. (2009). Social transmission of a host defense against cuckoo parasitism. *Science, 324*(5932), 1318–1320.

Davies, S., & Sewall, K. B. (2016). Agonistic urban birds: elevated territorial aggression of urban song sparrows is individually consistent within a breeding period. *Biology Letters, 12*, 20160315.

Deng, S. H., Lee, T. K., & Wee, Y. C. (2008). Black-naped terns (*Sterna sumatrana* Raffles, 1822) mobbing a grey heron (*Ardea cinerea* Linnaeus, 1758). *Nature in Signapore, 1*, 117–127.

Denson, R. D. (1979). Owl predation on a mobbing crow. *Wilson Bulletin, 91*(1), 133–133.

Dominey, W. J. (1983). Mobbing in colonially nesting fishes, especially the bluegill, *Lepomis macrochirus*. *Copeia, 1983*(4), 1086–1088.

Donaldson, T. J. (1984). Mobbing behavior by *Stegastes albifasciatus* (Pomacentridae), a territorial mosaic damselfish. *Japanese Journal of Icthology, 31*(3), 345–348.

Dow, D. D. (1977). Indiscriminate interspecific aggression leading to almost sole occupancy of space by a single species of bird. *Emu*, *77*(3), 115–121.

Dutour, M., Cordonnier, M., Lena, J.-P., & Lengagne, T. (2019). Seasonal variation in mobbing behaviour of passerine birds. *Journal of Ornithology*, *160*(2), 509–514.

Dutour, M., & Danel, S. (2020). Wild great tits' alarm calls prompt vigilant behaviours in free-range chickens. *Animal Cognition*, 1–4.

Dutour, M., Kalb, N., Salis, A., & Randler, C. (2021). Number of callers may affect the response to conspecific mobbing calls in great tits (*Parus major*). *Behavioral Ecology and Sociobiology*, *75*(2), 29.

Dutour, M., Lena, J.-P., & Lengagne, T. (2017). Mobbing behaviour in a passerine community increases with prevalence in predator diet. *Ibis*, *159*(2), 324–330.

Dutour, M., Lengagne, T., & Lena, J.-P. (2019). Syntax manipulation changes perception of mobbing call sequences across passerine species. *Ethology*, *125*(9), 635–644.

Dutour, M., & Randler, C. (2021). Mobbing responses of great tits (Parus major) do not depend on the number of heterospecific callers. *Ethology*, *127*(5), 379–384.

Ekman, J. (1986). Tree use and predator vulnerability of wintering passerines. *Ornis Scandinavica*, *17*(3), 261–267.

Engesser, S., Ridley, A. R., & Townsend, S. W. (2016). Meaningful call combinations and compositional processing in the southern pied babbler. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(21), 5976–5981.

Fang, W.-H., Hsu, Y.-H., Lin, W.-L., & Yen, S.-C. (2020). The function of avian mobbing: an experimental test of `attract the mightier' hypothesis. *Animal Behaviour*, *170*, 229-233.

Feeney, W. E., & Langmore, N. E. (2013). Social learning of a brood parasite by its host. *Biology Letters*, *9*(4), 20130443.

Ficken, M. S., & Popp, J. W. (1996). A comparative analysis of passerine mobbing calls. *The Auk*, *113*(2), 370–380.

Fishman, M. A. (1999). Predator inspection: closer approach as a way to improve assessment of potential threats. *Journal of Theoretical Biology*, *196*(2), 225–235.

FitzGibbon, C. D., & Fanshawe, J. H. (1988). Stotting in Thomson's gazelles: an honest signal of condition. *Behavioral Ecology and Sociobiology*, *23*(2), 69–74.

FitzGibbon, Clare D. (1994). The costs and benefits of predator inspection behaviour in Thomson's gazelles. *Behavioral Ecology and Sociobiology*, *34*(2), 139–148.

Flasskamp, A. (1994). The adaptive significance of avian mobbing. V. An experimental test of the move on hypothesis. *Ethology*, *96*(4), 322–333.

Foster, W. A., & Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, *293*, 466–467.

Francis, A. M., Hailman, J. P., & Woolfenden, G. E. (1989). Mobbing by Florida scrub jays: behaviour, sexual asymmetry, role of helpers and ontogeny. *Animal Behaviour, 38,* 795–816.

Frankenberg, E. (1981). The adaptive significance of avian mobbing. IV Alerting others and perception advertisement in blackbirds facing an owl. *Ethology*, *55*(2), 97–118.

Freeberg, T. M., & Lucas, J. R. (2002). Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*. *Animal Behaviour, 63,* 837-845.

Freeberg, T. M., & Lucas, J. R. (2012). Information theoretical approaches to chick-a-dee calls of Carolina chickadees (*Poecile carolinensis*). *Journal of Comparative Psychology*, *126*(1), 68–81.

Freeman, B. G., & Miller, E. T. (2018). Why do crows attack ravens? The roles of predation threat, resource competition, and social behavior. *The Auk*, *135*(4), 857–867.

Fuong, H., Keeley, K. N., Bulut, Y., & Blumstein, D. T. (2014). Heterospecific alarm call eavesdropping in nonvocal, white-bellied copper-striped skinks, *Emoia cyanura*. *Animal Behaviour*, *95*, 129–135.

Furrer, R. D., & Manser, M. B. (2009). Banded mongoose recruitment calls convey information about risk and not stimulus type. *Animal Behaviour*, *78*(1), 195–201.

Gehlbach, F. R., & Leverett, J. S. (1995). Mobbing of eastern screech-owls: predatory cues, risk to mobbers and degree of threat. *Condor*, *97*(3), 831–834.

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution*, *25*(6), 354–361.

Goodale, E., & Kotagama, S. W. (2005). Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. *Journal of Tropical Ecology*, *21*(6), 669–676.

Goodale, E., & Kotagama, S. W. (2006). Vocal mimicry by a passerine bird attracts other species involved in mixed-species flocks. *Animal Behaviour*, *72*, 471–477.

Goodale, E., & Kotagama, S. W. (2008). Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. *Behavioral Ecology*, *19*(4), 887–894.

Goodale, E., Ratnayake, C. P., & Kotagama, S. W. (2014). Vocal mimicry of alarm-associated sounds by a drongo elicits flee and mobbing responses from other species that participate in mixed-species bird flocks. *Ethology*, *120*(3), 266–274.

Goodale, E., & Ruxton, G. D. (2010). Antipredator benefits from heterospecifics. In M. D. Breed & J. Moore (Eds.), Encyclopedia of Animal Behavior (Vol. Volume 1, pp. 94–99). Academic Press, Elsevier.

Gottfried, B. M. (1979). Anti-predator aggression in birds nesting in old field habitats: an experimental analysis. *Condor*, *81*(3), 251–257.

Grabarczyk, E. E., & Ritchison, G. (2015). Vocal responses of adult Eastern bluebirds (*Sialia sialis*) to potential nest predators and the behavioral responses of nestlings. *The Wilson Journal of Ornithology*, *127*(4), 697–705.

Grabowska-Zhang, A. M., Sheldon, B. C., & Hinde, C. A. (2012). Long-term familiarity promotes joining in neighbour nest defence. *Biology Letters*, *8*(4), 544–546.

Grade, A. M., & Sieving, K. E. (2016). When the birds go unheard: highway noise disrupts information transfer between bird species. *Biology Letters*, *12*(4), 1–4.

Graw, B., & Manser, M. B. (2007). The function of mobbing in cooperative meerkats. *Animal Behaviour*, *74*(3), 507–517.

Griesser, M. (2008). Referential calls signal predator behavior in a group-living bird species. *Current Biology*, *18*(1), 69–73.

Griesser, M. (2009). Mobbing calls signal predator category in a kin group-living bird species. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 2887–2892.

Griesser, M., & Ekman, J. (2005). Nepotistic mobbing behaviour in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, *69*(2), 345–352.

Griesser, M., Mourocq, E., Barnaby, J., Bowgen, K. M., Eggers, S., Fletcher, K., Kozma, R., et al. (2017). Experience buffers extrinsic mortality in a group-living bird species. *Oikos*, *126*(9), 1258–1268.

Griesser, M., & Suzuki, T. N. (2016). Kinship modulates the attention of naive individuals to the mobbing behaviour of role models. *Animal Behaviour*, *112*(C), 83–91.

Griesser, M., & Suzuki, T. N. (2017). Naive juveniles are more likely to become breeders after witnessing predator mobbing. *The American Naturalist*, *189*(1), 58–66.

Griffin, A. S. (2004). Social learning about predators: a review and prospectus. *Learning & Behavior*, *32*(1), 131–140.

Griffin, A. S., & Jr, B. G. G. (2005). Social learning about predators: does timing matter? *Animal Behaviour*, *69*(3), 669–678.

Grim, T. (2007). Are blackcaps (*Sylvia atricapilla*) defending their nests also calling for help from their neighbours? *Journal für Ornithologie*, *149*(2), 169–180.

Grinnell, J. (1920). Sequestratioin notes. *Auk*, *XXXVII*, 84–88.

Gunn, J. S., Desrochers, A., Villard, M.-A., Bourque, J., & Ibarzabal, J. (2000). Playbacks of mobbing calls of black-capped chickadees as a method to estimate reproductive activity of forest birds. *Journal of Field Ornithology*, *71*(3), 472–483.

Gursky, S. (2006). Function of snake mobbing in spectral tarsiers. *American Journal of Physical Anthropology*, *129*(4), 601–608.

Gursky, S., & Nekaris, K. A. I. (2007). *Primate Anti-Predator Strategies*. (S. L. Gursky & K. A. I. Nekaris, Eds.) Springer. Springer.

Ha, J., Lee, K., Yang, E., Kim, W., Song, H. Ho-kyung, Hwang, I., Cruz, L. L., et al. (2020). Experimental study of alarm calls of the oriental tit (*Parus minor*) toward different predators and reactions they induce in nestlings. *Ethology*, *114*(4), 510–10.

Hailman, J. P., & Ficken, M. S. (1986). combinatorial animal communication with computable syntax: chick-a-dee calling qualifies as “language” by structural linguistics. *Animal Behaviour*, *34*(6), 1899–1901.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*, 295–311.

Hardman, S. I., & Dalesman, S. (2018). Repeatability and degree of territorial aggression differs among urban and rural great tits (*Parus major*). *Scientific Reports*, 1–12.

Hein, R. G. (1996). Mobbing behavior in juvenile French grunts (*Haemulon flavolineatum*). *Copeia*, *1996*(4), 989–991.

Hetrick, S. A., & Sieving, K. E. (2011). Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. *Behavioral Ecology*, *23*(1), 83–92.

Hinde, R. A. (1954a). Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*). I. The nature of the response, and an examination of Its course. *Proceedings of the Royal Society B: Biological Sciences*, *142*(908), 306–330.

Hinde, R. A. (1954b). Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*). II. The waning of the response. *Proceedings of the Royal Society of London*, *142*(908), 331–358.

Hinde, R. A. (1961). Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*) III. The interaction of short-term and long-term incremental and decremental effects. *Proceedings of the Royal Society B: Biological Sciences*, *153*(952), 398–420.

Hogan, B. G., Hildenbrandt, H., Scott-Samuel, N. E., Cuthill, I. C., & Hemelrijk, C. K. (2017). The confusion effect when attacking simulated three-dimensional starling flocks. *Royal Society Open Science*, *4*(1), 160564–9.

Hua, F., & Sieving, K. E. (2016). Understory avifauna exhibits altered mobbing behavior in tropical forest degraded by selective logging. *Oecologia*, *182*(3), 743–754.

Huang, P., Sieving, K. E., & Mary, C. M. S. (2012). Heterospecific information about predation risk influences exploratory behavior. *Behavioral Ecology*, *23*(3), 463–472.

Igic, B., & Magrath, R. D. (2014). A songbird mimics different heterospecific alarm calls in response to different types of threat. *Behavioral Ecology*, *25*(3), 538–548.

Ishihara, M. (1987). Effect of mobbing toward predators by the damselfish *Pomacentrus coelestis* (Pisces: Pomacentridae). *Journal of Ethology*, *5*(1), 43–52.

Ito, R., & Mori, A. (2010). Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard *Oplurus cuvieri cuvieri* (Reptilia: Iguania). *Proceedings of the Royal Society B: Biological Sciences*, *277*(1685), 1275–1280.

Jack, K. M., Brown, M. R., Buehler, M. S., Hernadez, S. C., Marín, N. F., Kulick, N. K., & Lieber, S. E. (2020). Cooperative rescue of a juvenile capuchin (*Cebus imitator*) from a Boa constrictor. *Scientific Reports*, 1–7.

Kalb, N., & Randler, C. (2019). Behavioral responses to conspecific mobbing calls are predator-specific in great tits (*Parus major*). *Ecology and Evolution*, *9*(16), 9207–9213. Retrieved from https://www.readcube.com/

Kastberger, G., Weihmann, F., Zierler, M., & Hötzl, T. (2014). Giant honeybees (*Apis dorsata*) mob wasps away from the nest by directed visual patterns. *Naturwissenschaften*, *101*(11), 861–873.

Kenward, R. E. (1978). Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *Journal of Animal Ecology*, *47*(2), 449–460.

Knight, R. L., & Temple, S. A. (1988). Nest-defense behavior in the red-winged blackbird. *Condor*, *90*(1), 193–200.

Krama, T., Bērziŋš, A., Rytkönen, S., Rantala, M. J., Wheatcroft, D. J., & Krams, I. A. (2011). Linking anti-predator behaviour and habitat quality: group effect in nest defence of a passerine bird. *Acta Ethologica*, *15*(1), 127–134.

Krams, I. A. (2001). Communication in crested tits and the risk of predation. *Animal Behaviour*, *61*(6), 1065–1068.

Krams, I. A., & Krama, T. (2002). Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, *Fringilla coelebs*. *Proceedings of the Royal Society of London*, *269*(1507), 2345–2350.

Krams, I. A., Krama, T., & Igaune, K. (2006). Mobbing behaviour: reciprocity-based co-operation in breeding pied flycatchers Ficedula hypoleuca. *Ibis*, *148*(1), 50–54.

Krams, I. A., Krama, T., Igaune, K., & Mänd, R. (2007). Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. *Behavioral Ecology*, *18*(6), 1082–1084.

Krams, I. A., Krama, T., & Iguaune, K. (2006). Alarm calls of wintering great tits Parus major: warning of mate, reciprocal altruism or a message to the predator? *Journal of Avian Biology*, *37*, 131–136.

Królikowska, N., Szymkowiak, J., Laidlaw, R. A., & Kuczyński, L. (2016). Threat-sensitive anti-predator defence in precocial wader, the northern lapwing Vanellus vanellus. *Acta Ethologica*, *19*, 163–171.

Lachat, J., & Haag-Wackernagel, D. (2016). Novel mobbing strategies of a fish population against a sessile annelid predator. *Scientific Reports*, *6*, 33187.

Leuchtenberger, C., Almeida, S. B., Andriolo, A., & Jr, P. G. C. (2016). Jaguar mobbing by giant otter groups. *Acta Ethologica*, *19*, 143–146.

Lima, H. S. de, Casas, F. M. G. L., Ribeiro, J. R., Souza, T. G., & Naka, L. N. (2018). Ecological and phylogenetic predictors of mobbing behavior in a tropical dry forest. *Ecology and Evolution*, *19*(24), 315–14.

Loughry, W. J. (1987). The dynamics of snake harassment by black-tailed prairie dogs. *Behaviour*, *103*(1–3), 27–47.

Lourenço, R., Penteriani, V., Delgado, M. del M., Marchi-Bartolozzi, M., & Rabaça, J. E. (2011). Kill before being killed: an experimental approach supports the predator-removal hypothesis as a determinant of intraguild predation in top predators. *Behavioral Ecology and Sociobiology*, *65*(9), 1709–1714.

Lucas, J. R., & Freeberg, T. M. (2007). “Information” and the chick-a-dee call: Communicating with a complex vocal system. Ecology and Behavior of Chickadees and Titmice (pp. 199–213). Oxford University Press.

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2014). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews*, *90*(2), 1–27.

Magrath, R. D., Haff, T. M., Horn, A. G., & Leonard, M. L. (2010). Calling in the Face of Danger Predation Risk and Acoustic Communication by Parent Birds and Their Offspring. *Advances in the Study of Behavior*, *41*, 187–253.

Magrath, R. D., Haff, T. M., & Igic, B. (2020). Interspecific Communication: Gaining Information from Heterospecific Alarm Calls. In T. Aubin & N. Mathevon (Eds.), Coding Strategies in Vertebrate Acoustic Communication (2nd ed., Vol. 7, pp. 287–314). Springer International Publishing.

Maklakov, A. A. (2002). Snake-directed mobbing in a cooperative breeder: anti-predator behaviour or self-advertisement for the formation of dispersal coalitions? *Behavioral Ecology and Sociobiology*, *52*(5), 372–378.

Manser, M. B., Jansen, D. A. W. A. M., Graw, B., Hollén, L. I., Bousquet, C. A. H., Furrer, R. D., & Roux, A. le. (2014). *Vocal Complexity in Meerkats and Other Mongoose Species*. Advances in the Study of Behavior Volume 22 (1st ed., Vol. 46). Elsevier Inc.

Marler, P. (1955). Characteristics of some animal calls. *Nature*, *176*(4470), 6–8.

Marler, P. (1957). Specific distinctiveness in the communication signals of birds. *Behaviour*, *11*(1), 13–39.

Marler, P. (1967). Animal communication signals. *Science*, *157*(3790), 769–774.

Marzluff, J. M., DeLap, J. H., & Haycock, K. (2015). Population variation in mobbing ospreys (*Pandion haliaetus*) by American crows (*Corvus brachyrhynchos*). *The Wilson Journal of Ornithology*, *127*(2), 266–270.

McDonald, P. G., Wilson, D. R., & Evans, C. S. (2009). Nestling begging increases predation risk, regardless of spectral characteristics or avian mobbing. *Behavioral Ecology*, *20*(4), 821–829.

Morris, D. (2009). *Owl*. London, UK: Reaktion Books Ltd.

Motta-Junior, J. C., & Santos-Filho, P. S. (2012). Mobbing on the striped owl (*Asio clamator*) and barn owl (*Tyto alba*) by birds in southeast Brazil: do owl diets influence mobbing. *Ornitología Neotropical*, *23*, 159–168.

Munoz, N., Brandstetter, G., Esgro, L., Greene, W., & Blumstein, D. T. (2015). Asymmetric eavesdropping between common mynas and red-vented bulbuls. *Behavioral Ecology*, *26*(3), 689–696.

Myers, J. P. (1978). One deleterious effect of mobbing in the Southern lapwing (*Vanellus chilensis*). *The Auk*, *95*(2), 419–420.

Němec, M., Syrová, M., Dokoupilová, L., Veselý, P., Šmilauer, P., Landová, E., Lišková, S., et al. (2014). Surface texture and priming play important roles in predator recognition by the red-backed shrike in field experiments. *Animal Cognition*, *18*(1), 259–268.

Ono, M., Igarashi, T., Ohno, E., & Sasaki, M. (1995). Unusual thermal defence by a honeybee against mass attack by hornets. *Nature, 377*, 334–336.

Owings, D. H., & Coss, R. G. (1977). Snake mobbing by California ground squirrels: adaptive variation and ontogeny. *Behaviour, 62*(1/2), 50–69.

Owings, D. H., Coss, R. G., Mckernon, D., Rowe, M. P., & Arrowood, P. C. (2001). Snake-directed antipredator behavior of rock squirrels (*spermophilus variegatus*): population differences and snake-species discrimination. *Behaviour*, *138*, 575–595.

Owings, D. H., & Loughry, W. J. (1985). Variation in snake-elicited jump-yipping by black-tailed prairie dogs: ontogeny and snake-specificity. *Zeitschrift für Tierpsychologie - Journal of Comparative Ethology, 70*, 177–200.

Owings, D. H., & Owings, S. C. (1979). Snake-directed behavior by black‐tailed prairie dogs (*Cynomys ludovicianus*). *Zeitschrift für Tierpsychologie*, *49*(1), 35–54.

Passamani, M. (1995). Field observation of a group of Geoffroy's marmosets mobbing a margay cat. *Folia Primatologica*, *64,* 163–166.

Pavey, C. R., & Smyth, A. K. (1998). Effects of avian mobbing on roost use and diet of powerful owls, *Ninox strenua*. *Animal Behaviour*, *55,* 313–318.

Pawlak, P., Kwieciński, Z., & Hušek, J. (2019). Mobbing of the top predator: a correlation between avian community richness and the number of mobbing species. *Journal of Ornithology*, *160*(3), 665–672.

Pettifor, R. A. (1990). The effects of avian mobbing on a potential predator, the European kestrel, *Falco tinnunculus*. *Animal Behaviour*, *39*(5), 821–827.

Rainey, H. J., Zuberbühler, K., & Slater, P. J. B. (2004). Hornbills can distinguish between primate alarm calls. *Proceedings of the Royal Society of London*, *271*(1540), 755–759.

Seeley, T. D., Seeley, R. H., & Akrathanaku, T. (1982). Colony defense strategies of the honeybees in Thailand. *Ecological Monographs*, *52*(1), 43–63.

Shedd, D. H. (1982). Seasonal variation and function of mobbing and related antipredator behaviors of the American robin (*Turdus migratorius*). *The Auk*, *99*(2), 342–346.

Shedd, D. H. (1983). Seasonal variation in mobbing intensity in the black-capped chickadee. *The Wilson Bulletin*, *95*(3), 343–348.

Sieving, K. E., Hetrick, S. A., & Avery, M. L. (2010). The versatility of graded acoustic measures in classification of predation threats by the tufted titmouse *Baeolophus bicolor*: exploring a mixed framework for threat communication. *Oikos*, *119*(2), 264–276.

Silvestri, A., Morgan, K., & Ridley, A. R. (2019). The association between evidence of a predator threat and responsiveness to alarm calls in Western Australian magpies

(*Cracticus tibicen dorsalis*). *PeerJ, 7*(7692), e7572-17. Retrieved from https://www.researchgate.net/

Smith, N. G. (1968). Provoked release of mobbing — a hunting technique of Micrastur falcons. *Ibis, 111*, 241–243.

Smythe, N. (1970). On the existence of "pursuit invitation" signals in mammals. *The American Naturalist, 104*(939), 491–494.

Sordahl, T. A. (1990). The risks of avian mobbing and distraction behavior: an anecdotal review. *The Wilson Bulletin, 102*(2), 349–352.

Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour, 78,* 337–347.

Sridhar, H., Jordán, F., & Shanker, K. (2013). Species importance in a heterospecific foraging association network. *Oikos, 122*(9), 1325–1334.

Suzuki, T. N. (2011). Parental alarm calls warn nestlings about different predatory threats. *Current Biology, 21*(1), R15–R16.

Suzuki, T. N. (2012). Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. *Animal Behaviour, 84*(1), 53–57.

Suzuki, T. N. (2014). Communication about predator type by a bird using discrete, graded and combinatorial variation in alarm calls. *Animal Behaviour, 87*, 59–65.

Suzuki, T. N. (2015). Assessment of predation risk through referential communication in incubating birds. *Scientific Reports, 5,* 1–6.

Suzuki, T. N. (2016). Referential calls coordinate multi-species mobbing in a forest bird community. *Journal of Ethology, 34*(1), 79–84.

Suzuki, T. N. (2018). Alarm calls evoke a visual search image of a predator in birds. *Proceedings of the National Academy of Sciences of the United States of America, 115*(7), 1541–1545.

Suzuki, T. N. (2021). Animal linguistics: Exploring referentiality and compositionality in bird calls. *Ecological Research, 36*, 221–231.

Suzuki, T. N., & Ueda, K. (2013). Mobbing calls of Japanese tits signal predator type: field observations of natural predator encounters. *The Wilson Journal of Ornithology, 125*(2), 412–415.

Suzuki, T. N., Wheatcroft, D., & Griesser, M. (2017). wild birds use an ordering rule to decode novel call sequences. *Current Biology, 27*(15), 2331-2336.e3.

Suzuki, T. N., Wheatcroft, D. J., & Griesser, M. (2016). Experimental evidence for compositional syntax in bird calls. *Nature Communications, 7,* 1–7.

Tamura, N. (1989). Snake-directed mobbing by the Formosan squirrel *Callosciurus erythraeus thaiwanensis*. *Behavioral Ecology and Sociobiology*, *24*(3), 175–180.

Templeton, C. N., & Carlson, N. V. (2019). Communication Networks. In J. C. Choe (Ed.), Encyclopedia of Animal Behavior (2nd ed., pp. 568–580). Elsevier Academic Press.

Templeton, C. N., & Greene, E. (2007). Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(13), 5479–5482.

Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science*, *308*(5730), 1934–1937.

Templeton, C. N., Zollinger, S. A., & Brumm, H. (2016). Traffic noise drowns out great tit alarm calls. *Current Biology*, *26*(22), R1173–R1174.

Tórrez, L., Robles, N., González, A., & Crofoot, M. C. (2012). Risky Business? Lethal attack by a jaguar sheds light on the costs of predator mobbing for capuchins (*Cebus capucinus*). *International Journal of Primatology*, *33*(2), 440–446.

Trnka, A., Prokop, P., & Grim, T. (2012). Uncovering dangerous cheats: how do avian hosts recognize adult brood parasites? *PLoS ONE*, *7*(5), e37445.

Vieth, W., Curio, E., & Ernst, U. (1980). The adaptive significance of avian mobbing. III. Cultural transmission of enemy recognition in blackbirds: cross-species tutoring and properties of learning. *Animal Behaviour*, *28*(4), 1217–1229.

Vitousek, M. N., Adelman, J. S., Gregory, N. C., & Clair, J. J. H. S. (2007). Heterospecific alarm call recognition in a non-vocal reptile. *Biology Letters*, *3*(6), 632–634.

Vrublevska, J., Krama, T., Rantala, M. J., Mierauskas, P., Freeberg, T. M., & Krams, I. A. (2014). Personality and density affect nest defence and nest survival in the great tit. *Acta Ethologica*, *18*(2), 111–120.

Wilson, D. R., & Hare, J. F. (2006). The adaptive utility of Richardson’s ground squirrel (*Spermophilus richardsonii*) short-range ultrasonic alarm signals. *Canadian Journal of Zoology*, *84*(9), 1322–1330.

Woods, R. D., Kings, M., McIvor, G. E., & Thornton, A. (2018). Caller characteristics influence recruitment to collective anti-predator events in jackdaws. *Scientific Reports*, *8*(1), 7343.

Zahavi, A. (1977). The cost of honesty further remarks on the handicap principle. *Journal of Theoretical Biology*, *67*(3), 603–605.