

PREY RESPONSES TO  
DISTURBANCE CUES:  
EFFECTS OF  
FAMILIARITY, KINSHIP,  
AND PAST EXPERIENCE  
WITH RISK

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By

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## Abstract

Prey can acquire information about predators by eavesdropping on conspecific cues, but these cues are not always reliable. In aquatic systems, disturbance cues are pulses of urea or ammonia that are often released by prey while fleeing a predator; nearby individuals typically display antipredator responses after detecting these cues. Despite the importance of disturbance cues to aquatic prey survival, they remain largely understudied in terms of their function and evolution. Here, I sought to test whether disturbance cues might function as an antipredator signal. Using a series of experiments, I assessed how familiarity and relatedness with individuals releasing the cues affects the antipredator response of the receiver, and whether background risk levels for the cue releaser and receiver play a role in the response exhibited by the receiver. If prey rely more on disturbance cues from familiar, related, or high predation risk background conspecifics, then I expect to see a heightened fright response to these cues. To test this, I raised wood frog (*Lithobates sylvaticus*) egg clutches and obtained disturbance cues from groups of tadpoles by simulating a predator chase. Counter to expectation, tadpoles exposed to disturbance cues from unfamiliar individuals displayed a fright response, whereas disturbance cues from familiar individuals were ignored, possibly because these cues became unreliable after being detected repeatedly in the absence of a true threat. Tadpoles responded similarly to the disturbance cues of related and unrelated individuals, suggesting that related individuals did not provide more reliable information. When manipulating background predation risk, high-risk receivers but not low-risk receivers responded to disturbance cues from low-risk donors, suggesting a lower response threshold in high-risk prey. Disturbance cues from high-risk donors also elicited more of a fright response in both high- and low-risk receivers. This suggests that high-risk prey release more, or more potent disturbance cues. Taken together, these experiments provide strong evidence that tadpoles detect variation in disturbance cues and may be capable of modulating their disturbance cues as antipredator signals. These findings are of important consideration for conservationists studying how Allee effects manifest in threatened aquatic species such as anuran tadpoles.

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## **Dedication**

Threefold:

To my parents.

To R, my one true love.

To Justin Trudeau, my eternal doppelgänger.

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## Chapter 1: Introduction

### 1.1. Animal communication

Communication is fundamental for any relationship, be it among friends or family, and through good and bad times. Both humans and many non-human animals rely on social communication as a source of information to make decisions about where to forage, with whom to mate and what is dangerous (Bradbury and Vehrencamp 2011). E.O. Wilson (1975) defined communication as the behaviour of an individual that changes the likely behaviour of another in a way that may benefit either party. Therefore communication, by definition, may be unreliable or dishonest. Individuals that provide reliable and accurate information are more likely to be acknowledged and be cooperated with in the future (Trivers 1971; Milinski et al. 1990; Dugatkin and Alfieri 1991). On the contrary, individuals that are unreliable or misleading may be subject to the ire, avoidance, or will simply be ignored by other individuals (Clutton-Brock and Parker 1995; Hare and Atkins 2001; Blumstein et al. 2004). Another inference from this definition is that there are three potential payoff schemes of communication: either both parties benefit (i.e., honest communication by the sender), the initial individual who elicited the first behaviour benefits (i.e., manipulation/deceit by the sender), or only the receiver of the communicated message benefits (i.e., cue eavesdropping by the receiver) (Wilson 1975; Marler 1977; Krebs and Dawkins 1984).

Cue eavesdropping involves unintentional or incidental stimuli known as cues that can be used as a source of information and which guide future actions of the receivers (Otte 1974; Hasson 1994). For example, mosquitoes cue in on CO<sub>2</sub> gas and other chemicals released through exhalation and sweating by mammals in order to home in on their next blood meal (Donath 2007). In contrast, signals are features shaped and maintained by natural selection over the course of evolution that now have an intended message for receivers, and which modify receiver behaviour in a way that benefits the sender (Otte 1974; Hauser 1996; Seyfarth and Cheney 2003;

Donath 2007). Honest signals (+ / + [sender/receiver] payoff) include those used in foraging and antipredator behaviours. For example, cliff swallows (*Hirundo pyrrhonota*) cooperatively track and forage on swarms of insects using squeak calls to recruit others to aid them in their pursuit (Brown et al. 1991). Damp wood termites (*Zootermopsis angusticollis*) emit a contagious vibrational alarm signal by repeatedly striking their heads against the substrate (Howse 1964; Kirchner et al. 1994). However, ‘true’ signalling also includes manipulation of the receiver by the sender (Marler 1977). Piping plovers (*Charadrius melodus*) manipulate their predators by leading them away from their nest and feigning an injured wing until they eventually fly off from the predator (Ristau 1993). One key difference between signals and cues is the intentionality implied by a signal, whereas cues are incidentally produced. Yet, experimentally demonstrating intentionality in non-human animals is extremely difficult, requiring complex, convoluted experiments (see Vauclair 1997). Additionally, it is debated in the literature as to whether signals encompass any information at all (see Scott-Phillips 2016 for a review).

In this thesis, I adopt the previously-described definitions of signal and cue (Donath 2007; Otte 1974). Responding to a signal would imply that the behaviour of the receiver is expected to change in such a way that the sender incurs some overall fitness benefit and is capable of manipulating the signal based on the perceived audience. I define the emitters of signals vs. cues as ‘senders’ and ‘donors’, respectively, and the individual(s) detecting them as ‘receivers’.

## **1.2. Evolution of signals**

Many signals are thought to have evolved from cues through cue ritualization. During cue ritualization, receivers begin taking advantage of the raw cues produced incidentally in association with another event and form an incidental association of the cue and the event (Bradbury and Vehrencamp 2011). Through natural selection, the receivers then develop better sensory mechanisms to better detect these cues while the cue donor begins amplifying the cue released (Tinbergen 1952), also known as ‘spying’ (*sensu* Sorensen and Stacey 1999). If the fitness of the cue donor is enhanced when receivers detect their cues, selection will drive sensory refinement of the donor’s cues to increase their range and amount of information that they contain. Eventually through co-evolutionary refinement, the cues themselves are ‘emancipated’ from their original roles to form a novel signalling system (Tinbergen 1952; Bradbury and

Vehrencamp 2011). While most examples of cue ritualization are based on comparative studies and are largely speculative, it is hypothesized that scent marking in canids evolved in this way. When young pups meet new conspecifics, they become excited and often incontinent. Soon, this cue of urination became associated with meeting novel dogs, and eventually became involved with maintaining territories in dogs and wolves (Morris 1956; Bradbury and Vehrencamp 2011). Additionally, the 'hair on end' posture of cats and other felids is likely to have evolved from the pairing of a stressful event with the piloerection of hairs used to cool down the animal upon overheating, resulting in a signal of the cat's agitation in order to dissuade potential aggressors (Bradbury and Vehrencamp 2011). Finally, the large, inflatable gular sacs used in mating courtship by male tetraonids (grouse and partridge family) likely evolved via the increased respiration rates during intrasexual competitive bouts among males (Bradbury and Vehrencamp 2011).

Vestigial signals that have lost their original function can also be repurposed in a process called signal exploitation. For example, nocturnal butterflies of the family Arctiidae use ultrasonic hearing and their own brand of ultrasound to confuse bat predators (Miller 1991; Corcoran 2013), but in some populations with fewer or no bat predators, these individuals have shifted their vestigial ultrasonic jamming abilities towards courtship communication functions (Conner 1987; Muma and Fullard 2004; Nakano et al. 2009).

Signalling mechanisms can also evolve through sexual selection. Fisher (1930) predicted that sexual selection would result in increasingly accentuated and ornate traits that eventually evolve past the point of practicality in a process called runaway selection. Zahavi's Handicap Principle (1975) involves the evolution and maintenance of costly and impractical traits that act as 'handicaps', and thus are viewed by the opposite sex as an honest indication of mate quality, since low quality individuals cannot afford these handicaps. The Handicap Principle also predicts that costly but honest behaviours will be maintained. Purportedly altruistic behaviour may even result from this process, as mates with high 'social prestige' may be preferred over others that do not aid others altruistically (Wright 1999). Food sharing, for example, is a seemingly altruistic trait that is maintained in part through sexual selection. Even in humans, altruistic men are more attractive to women (Phillips et al. 2010).

### 1.3. Alarm signals

Another prime example of a seemingly altruistic behaviour is alarm signalling of predators by group-living prey. Alarm signalling is seemingly maladaptive to the sender, since they may more easily be detectable by predators and thus more vulnerable (Maynard Smith 1965). Alarm signalling takes place across many sensory modalities, such as acoustic alarm calls in rodents (e.g., Shelley and Blumstein 2004), visual fin-flicks in tetras (*Hemigrammus erythrozonus*) (Brown et al. 1999), and olfactory/chemical pheromones in bees (Alaux and Robinson 2007). Through collective vigilance and alarm signalling, groups of prey can decrease their time spent vigilant of predators and spend more time foraging (Lima 1995; Roberts 1996).

Alarm signals can encompass a great diversity of information regarding the predator, including the specific type of predator, their relative direction or position from the alarm caller, and their relative risk. Vervet monkeys (*Chlorocebus pygerythrus*) and other mammals use functionally-referent alarm calls to distinguish different prey types that, when received, prompt a specific antipredator response to the type of predator that is nearby (Seyfarth et al. 1980; Slobodchikoff et al. 1991; Evans et al. 1993; Blumstein and Arnold 1995; Kiriazis and Slobodchikoff 2006). For example, vervets produce specific calls towards avian predators, large mammalian predators, and snake predators (Seyfarth et al. 1980). Calls also can be used to determine the relative position and/or direction of the predator. For example, Richardson's ground squirrels (*Urocitellus richardsonii*) perceiving the calls of multiple individuals can infer the moving position of a predator and adjust their vigilance accordingly (Thompson and Hare 2010). Finally, alarm signals and cues often inherently communicate the intensity of predation threats. Therefore, receivers are expected to respond to signals and cues in a graded or 'threat-sensitive' manner according to the intensity of the signal or cue (Blumstein 1995; Blumstein and Arnold 1995; Warkentin et al. 2001). In addition to past experiences with the sender of the signal and the information encoded within the signal itself, receivers also weight their response intensity on contextual information about the environment and its relative risk.

Individuals are more likely to heed the warnings of conspecific alarm signals and cues when they are in agreement with other environmental stimuli predicting predation risk. According to the 'sensory complementation' hypothesis, predation risk is best approximated from as many modalities and sources as possible (Lima and Steury 2005). Even when signals and cues indicating risk disagree with one's own personal experience, signals and cues may override

personal experience, resulting in individuals learning to avoid a stimulus that they had previously learned to ignore (Vieth et al. 1980; Mineka and Cook 1986; Crane and Ferrari 2015). When signals or cues from different sources do not agree, the ‘flag model’ of signal/cue reliability suggests that individuals will respond to the signals/cues of others only if they have been more reliable than other stimuli, such as environmental, spatial, or temporal cues, but not otherwise (McLinn and Stephens 2006; Polnaszek and Stephens 2014; Heinen and Stephens 2016). The ‘costly information hypothesis’ predicts that prey rely more on social information when the costs of obtaining further information (through direct experience with predators) are high (Boyd and Richerson 1985). For instance, prey from environments with many predators may rely more on social information from conspecifics (signals and cues) relative to prey from environments with relatively few predators and thus lower risk (Webster and Laland 2008).

#### **1.4. Kin selection and recognition**

W.D. Hamilton (1964) first suggested that genes could themselves promote seemingly altruistic behaviour such as alarm signalling. Hamilton’s rule states that a gene promoting ‘altruistic’ behaviour will increase in frequency when the indirect fitness benefits ( $B$ ) multiplied by the coefficient of relatedness ( $r$ ) outweigh the direct costs to the emitter of the behaviour ( $C$ ). Hence the equation:  $rB > C$ , where the coefficient of relatedness  $r$  is the expected proportion of genetic similarity to the recipient(s) of the ‘altruistic’ behaviour. Empirically, Hamilton’s rule has been supported by several studies (Gorrell et al. 2010; Mateo 2015), most notably, North American red squirrels (*Tamiasciurus hudsonicus*) appear to adopt only individuals that are somewhat related to themselves. However, in some species, familiarity with kin is a requirement to incur the benefits of kin selection (e.g., Hare and Murie 1996; Frommen et al. 2013; Mateo 2017). At the same time as Hamilton’s rule, Maynard Smith (1964) coined the term ‘kin selection’, predicting that animals could gain the greatest biological fitness benefits by maximizing not only their direct fitness associated with their own offspring, but also their indirect fitness from their aunts, uncles, cousins, nieces, and nephews who all share some proportion of their genetics.

Recognition of kin is theorized to occur either based on spatial location, familiarity (past experience), phenotype/template matching, and/or recognition alleles (i.e., the greenbeard effect) (Hamilton 1964; Blaustein 1983). For example, bank swallows (*Riparia riparia*) may use the

spatial location of their nests to differentiate their offspring from others' offspring at first, prior to fledging (Beecher et al. 1981). After fledging, the parents become attuned to the 'signature' calls of their offspring. This type of recognition involving differentiating previously experienced stimuli (familiar) from unfamiliar stimuli that have never been encountered before is called familiarity-based kin recognition. Familiarity-based recognition is often tested using a cross-fostering design, where individuals from different clutches are swapped at birth and raised by a non-kin mother, then exposed to stimuli from both unfamiliar and familiar, kin and non-kin (Holmes and Sherman 1982). If the individuals being tested respond amicably to both familiar kin and non-kin relative to all unfamiliar individuals, familiarity-based kin recognition is likely occurring – as is the case in guppies (*Poecilia reticulata*) (Griffiths and Magurran 1999b). However, if unfamiliar and familiar kin are treated similarly, then kin recognition through phenotype matching or recognition alleles is likely occurring. These mechanisms are the most accurate form of kin recognition, and thus are favoured to evolve whenever multiple mating, cooperative breeding, inter-/intra-specific parasitism, or large group sizes occur (Holmes and Sherman 1982). Phenotype matching (sometimes called 'template matching') involves using certain individuals' stimuli as templates for what all kin look like (Holmes and Sherman 1982). For instance, zebrafish (*Danio rerio*) likely use olfactory imprinting within the first 24 hours after birth to determine kin templates that they go on to use for the rest of their lives when sorting conspecifics as either kin or non-kin. Animals can also recognize kin through phenotype matching by using their own phenotype as a reference, and this is termed self-referent phenotype matching. Moreover, Belding's ground squirrels (*Urocitellus beldingi*) may use self-referent phenotype matching in the month after birth, since individuals with manipulated personal odours classify kin differently than naturally kept individuals (Mateo 2010; Mateo 2017). Finally, recognition alleles involve specific gene alleles that manifest as some recognizable phenotype (e.g., Dawkin's 'green-beard' phenotype) and predispose the behaviour of the bearer to favour others with this unique phenotype and recognition allele (Dawkins 1976; Blaustein 1983). Evidence of recognition alleles includes alleles of the *Gp-9* locus in fire ants (*Solenopsis invicta*), which dictates whether colonies have one or many queens (Krieger and Ross 2002). Distinguishing between self-referent phenotype matching or recognition allele mechanisms is extremely difficult, and the differences manifesting from the two are trivial anyhow (Blaustein 1983; Hare et al. 2003).



Regardless of mechanisms, once kin are recognized, kin-biased behaviour serves to increase the overall biological fitness of related individuals, and thus inclusive fitness. Some classic examples of kin-biased behaviour include aunting and helping behaviour in primates and birds (Riedman 1982; Fairbanks 1990), non-sibling-biased cannibalism in plains spadefoot toad (*Spea bombifrons*) tadpoles (Pfennig et al. 1993), and association preferences and amicable behaviour being directed towards kin. The latter is seen in many species, especially early on in development (Krause et al. 2000; Gerlach and Lysiak 2006).

### **1.5. Reciprocal altruism and byproduct mutualism**

Where repeated encounters among individuals occur, reciprocally altruistic behaviours may evolve to maximize cumulative fitness payoffs over the long term. These ‘evolutionarily stable strategies’ were first demonstrated by repeated game theoretical models using the Prisoner’s Dilemma (Axelrod et al. 1981; Brems 1996), and further backed by empirical observations (Cheney and Seyfarth 1988; Stoddard et al. 1990; Robert E. Johnston 1994). Reciprocal altruism is the process by which an individual decreases their immediate fitness in order to increase the fitness of another individual (- / +) with the expectation of future fitness increasing (Trivers 1971). It is hypothesized that reciprocal altruism aids in maintaining ‘altruistic’ behaviours such as alarm signalling (Maynard Smith 1965). In contrast, byproduct mutualism arises when individuals cooperate for their own individual benefits (+ / +) (West Eberhard 1975), as is likely the case for ‘dear enemy’ recognition in birds, where neighbours habituate to one another and de-escalate aggression against one-another to save time and energy (Fisher 1954; see Moser-Purdy and Mennill 2016 for a review). Yet, ‘dear enemy’ neighbours may also engage in coordinated mobbing against nest predators (Getty 1987), which more exemplifies reciprocal altruism rather than byproduct mutualism. Interestingly, individuals that break the ‘neighbourly trust’ by intruding on a neighbour’s territory or mating with their neighbour’s partner often face increased aggression after trespassing relative to unfamiliar individuals (Olendorf et al. 2004). This is predicted by game theoretical models, where the optimal strategy to adopt when repeatedly interacting with others is a ‘tit for tat’ strategy, where individuals reciprocate the past actions of others (Axelrod et al. 1981). ‘Tit for tat’ is commonplace in the wild, but may require individual recognition of others (Axelrod et al. 1981; Milinski 1987; Milinski et al. 1990). For example, tufted capuchins (*Cebus apella*) share their

food reward with conspecifics who have aided them in the past, and individuals are more likely to cooperate with other capuchins that had rewarded them with food sharing in the past (De Waal and Berger 2000). These individual recognition mechanisms appear to operate in a variety of different vertebrate taxa in order to recognize others and remember their past behaviour (e.g., Belcher and Thompson 1969; Emlen 1971; Wooller 1978; Myrberg and Riggio 1985; Robert E. Johnston 1994; Hare and Atkins 2001; Lovell 2003; Blumstein et al. 2004; Wiley 2005; Carazo et al. 2008; Briseño-Jaramillo et al. 2014), and are expected to evolve when the cost of deception is relatively high over the long-term (Koops 2004). However, one cognitive shortcut for detecting individual reliability may be familiarity, where individuals tend to favour others with whom they have previous experience (Archawaranon et al. 1991). Below, I explore how familiarity and genetic relatedness bias individual and group behaviour, and how they are often confounded.

## **1.6. Familiarity and Kinship**

For simplicity, I define familiarity as individuals that have had much more relative experience with one another, relative to so-called unfamiliar individuals, while I define kinship as individuals having substantial genetic relatedness to one-another (coefficient of relatedness,  $r \geq 0.1$ ). However, being familiar and being related are usually not mutually exclusive, and studies of one tend to confound the other in the literature (Penn and Frommen 2010). For example, kinship is dependent on familiarity in some species using familiarity-based phenotype matching (e.g., Griffiths and Macgurrán 1999), but may be independent of familiarity in species using phenotype matching or recognition alleles (e.g., Le Vin et al. 2010; Frommen et al. 2013). Studies attempting to separate the two can consider cross-fostering designs (as discussed in 1.4), or simply study each separately while holding the condition of the other constant. Seppä et al. (2001) did the latter by artificially creating groups of unrelated Arctic char (*Salvelinus alpinus*) at birth, and rearing them together over a 21-day period to test for differences strictly associated with familiarity. Alternatively, if Arctic char are separated during egg development, kinship effects can be studied by examining differences in char interactions with unfamiliar kin and unfamiliar non-kin (Winberg and Håkan Olsén 1992; Håkan Olsén and Winberg 1996). In these examples, juvenile Arctic char do better when reared in unrelated familiar groups, and do not significantly prefer unfamiliar kin over non-kin.

The process of familiarization varies among species, both in terms of the time it takes to become 'familiar' and lose familiarity preferences, as well as in the sensory modality used for recognizing familiar conspecifics. Familiarization with kin often occurs rapidly early on in development (Brown and Brown 1996; Mateo 2010; Mateo 2017), while familiarization with a non-kin group ranges from hours to months (Griffiths and Magurran 1997; see Griffiths 2003 for a review). Familiarization may occur through odour (e.g., Van Havre and FitzGerald 1988; Brown and Smith 1994; Håkan Olsén and Winberg 1996; Coffin et al. 2011), visually (e.g., Arduini 2016), acoustically (e.g., Brooks and Falls 1975; Myrberg and Riggio 1985; Wiley 2005), or through some combination of stimuli (e.g., Griffiths and Magurran 1999). Despite the rapid acquisition of familiarity preferences in many species, familiarity effects can quickly be lost if conspecifics are not interacting regularly. Johnsson (1997) reported similar aggression levels towards unfamiliar and familiar individuals when familiar rainbow trout shoalmates were separated for 3+ days from each other. Other species appear to remember shoalmates long after separation, with guppies and fathead minnows preferentially associating with familiars 5 weeks and 2 months after separation, respectively (Brown and Smith 1994; Bhat and Magurran 2006). The difference may be due to a difference in ecology, with territorial species such as salmonids quickly forgetting their familiar neighbours while shoaling fish must rely more on their familiar shoalmates for increased survival, and thus remember them for longer (Chivers et al. 1995; Griffiths 2003).

For many species, the preference for familiarity also depends on resource context and group size. Webster and Hart (2006) found that the positive effects of familiarity are only seen when food sources are more dispersed, rather than found clumped together. Satiation levels have been shown to affect the preference for familiar or similar individuals, with individuals reversing their preference for both when they are starved (Reebs and Saulnier 1997; Frommen et al. 2007). Most fish have a preference for familiar and larger shoals, but familiar shoals will be preferred over unfamiliar but larger shoals up to twice as large (Barber and Wright 2001). Moreover, familiarity preferences in wild populations is much less commonly documented, possibly because wild individuals may interact with many more conspecifics than in the laboratory setting (Krause et al. 2000; Griffiths 2003). Familiarity preferences and social benefits of familiarity tend to decrease with increasing group size, suggesting that familiarity is easier to maintain and/or more important for smaller populations rather than larger ones (Griffiths and Magurran

1997a; Schweitzer et al. 2011). Additionally, familiarity preferences appear to be strongest in species with high site or shoal fidelity, such as coral reef fishes and song birds, where repeat encounters result in dear enemy recognition (Krause et al. 2000; Moser-Purdy and Mennill 2016).

In terms of kin-biased preferences, the results are even more convoluted. For example, many laboratory studies find kinship effects when familiarity is not controlled (Krause et al. 2000; Griffiths 2003; Penn and Frommen 2010). Yet, most field studies on adult animals show no preference for kin, and some species even display a preference for non-kin associations (Hare 1992; Hare and Murie 1996; Behrmann-Godel et al. 2006; Croft et al. 2012). This suggests that where kinship preferences are detected, they may be the direct result of unnatural conditions experienced in the laboratory setting (Krause et al. 2000; Penn and Frommen 2010). Avoiding kin as adults is presumably to increase mating opportunities and avoid inbreeding, or may aid with dispersal (Hare 1992; Coffin et al. 2011; Bonadonna and Sanz-Aguilar 2012). Interestingly, the degree of nepotism shown towards kin depends on the species; for example, Columbian ground squirrels (*Urocitellus columbianus*) only extend kin-biased behaviour towards closely-related relatives ( $r \geq 0.25$ ), i.e., mothers, daughters, sisters, and half-sisters (Sherman 1981), while black-tailed prairie dogs (*Cynomys ludovicianus*) extend similar kin-biased behaviour to all their close and distant kin regardless of the degree of relatedness (Hoogland 1986). Species using self-referent phenotype matching often exhibit a lagged kin-biased preference, as they require time to form their kin templates (Gerlach et al. 2008; Sikkel and Fuller 2010; Hesse et al. 2012; Mateo 2017).

Familiarity among group members has a plethora of benefits relative to unfamiliar individuals, in both foraging and antipredator contexts. Familiarity with others generally reduces aggression and density-dependent stress, as seen with dear enemy recognition (Ferkin 1988; Höjesjö et al. 1998; Puppe 1998; Utne-Palm and Hart 2000; Gómez-Laplaza 2005; Závorka et al. 2015). However, familiarity with group members may benefit individuals in terms of increased foraging time (Höjesjö et al. 1998; Griffiths et al. 2004; Morrell et al. 2008; Liebgold and Dibble 2011), faster growth (Seppä et al. 2001; Závorka et al. 2015), and faster social learning (Lachlan et al. 1998; Swaney et al. 2001; Kavaliers et al. 2005; Morrell et al. 2008; Atton et al. 2014). Familiarity aids to increase the frequency of cooperative behaviours that bolster individual survival and reproductive success (Beletsky and Orians 1991; König 1994; Höjesjö et al. 1998;

Grabowska-Zhang et al. 2012), even when groups are composed of entirely unrelated conspecifics (Seppä et al. 2001). For instance, juvenile European catfish (*Silurus glanis*) in familiar groups better monopolize shelter space relative to unfamiliar catfish (Slavík et al. 2012). Familiarity can even be used to predict long-term measures of fitness, such as overwintering clutch success. For example, long-term social network studies of brown-headed cowbirds (*Molothrus ater*) reveal that the degree of association with familiar conspecifics is consistent through time, and familiarity with others (measured in the fall) is also the best predictor of larger clutch sizes the following spring (Kohn et al. 2015; Kohn 2017). Despite these many benefits, familiarity may not be preferred in certain contexts, such as when selecting a mate (e.g., Kelley et al. 1999).

There are many examples of kin-biased behaviour and benefits associated with living in groups of predominantly kin. Kin-dominated groups have similar benefits to familiar groups, including reduced aggression (Sikkel and Fuller 2010; Griesser et al. 2015), increased growth (Thünken et al. 2016), faster social learning (Kavaliers et al. 2005), increased cooperation in risky behaviours (Krause et al. 2000; Hesse et al. 2015), and overall increased survival (de Bruijn et al. 2014). Additionally, alloparental care and adoption are more likely when the adopting parent is at least partially related to the orphaned juvenile (e.g., Riedman 1982; Gorrell et al. 2010; Thorington and Weigl 2011). Finally, alarm signalling may be used increasingly when kin are nearby. Sherman (1985) reported increased alarm calling in reproductive females with extant offspring or other descendants nearby relative to mothers without offspring.

When it comes to alarm signalling in aquatic animals and the effects of familiarity and kinship, relatively few studies exist. Despite the lack of observations, it is likely that many aquatic signals and cues may be biased towards familiar and/or genetically-related conspecifics.

### **1.7. Communication of risk in aquatic environments**

Group-living animals can perceive many cues from others that represent an important source of information regarding their environment's potential dangers (Lima 1995; Roberts 1996; Dall 2010). For example, predator detection is increased through collective group vigilance in many group-living animals. By monitoring the social cues of neighbours, individuals reduce their energetic costs associated with remaining vigilant (Lima 1995; Roberts 1996; Rieucau and Giraldeau 2011). Prey can also rapidly learn novel threats in their environment

simply by observing and copying the behaviour of others (Rendell et al. 2010; Crane et al. 2012; Hogan and Laskowski 2013; Hoppitt and Laland 2013; Smolla et al. 2016).

In the context aquatic environments, aquatic cues may be perceived through multiple sensory modalities, including visual, mechanical, and chemical stimuli. Fish can learn a predator from visual conspecific cues on their own (Magurran and Higham 1988; Hogan and Laskowski 2013), and even in total darkness, fish are able to learn a predator when in the presence of predator-experienced conspecifics through chemical and/or mechanical conspecific stimuli (Manassa et al. 2013). Tadpoles can also locate and learn food and predator stimuli via the social cues of others, and this likely involves both visual and mechanical stimuli resulting from nearby conspecifics' locomotion (Sontag et al. 2006; Ferrari et al. 2007; Ferrari and Chivers 2008), in addition to the chemical cues emitted (Gonzalo et al. 2010; Crane and Ferrari 2013).

In the context of predation, there are three general chemical cues that prey can use to detect and avoid being eaten. First, the predator themselves may emit their own predator odour, which may include diet cues from previously digested conspecifics (Mitchell et al. 2017). Second, as the prey is chased by the predator, they also release chemical disturbance cues, which are likely metabolite byproducts released by uninjured conspecifics when startled and/or chased by predators, or presumably through chasing by dominant conspecifics or other abiotic disturbances (Hazlett 1990a; Bryer et al. 2001; Ferrari et al. 2010; Mitchell et al. 2017). Finally, when aquatic prey succumb to injury or parasitism causing tissue damage, chemical alarm cue or 'Schreckstoff' is released and becomes a cue representing certain predation risk (von Frisch 1942; Chivers et al. 2007; Ferrari et al. 2010). Focusing on the latter two, both alarm and disturbance cues elicit behavioural responses in aquatic prey, usually consisting of reduced activity and foraging (Smith 1992; Wisenden et al. 1995; Kiesecker et al. 1999; Bryer et al. 2001; Ferrari et al. 2008; Ferrari et al. 2010; Gonzalo et al. 2010) and produce physiological stress responses in some fish species (Toa et al. 2004; Bett et al. 2016).

Both alarm and disturbance cues present important information regarding the environment's predation risk, however, their level of plasticity and reliability differ as a result of differences in each cues' production. Since alarm cues are released as a result of at least partially successful predation, they are unlikely to be released unreliably, whereas disturbance cues may be released voluntarily and thus are subject to being unreliably deployed by conspecifics (Fraker et al. 2009; Ferrari et al. 2010; Mitchell et al. 2017). As a corollary to this, prey generally elicit

less of an antipredator response to disturbance cues relative to alarm cues (Mirza and Chivers 2002a; Ferrari et al. 2008; Gonzalo et al. 2010), and responses to predator odours are greater when they are learned in association with alarm cues rather than disturbance cues (Ferrari et al. 2008; Gonzalo et al. 2010). Regardless, it is unlikely that alarm cues have evolved as conspecific alarm signals, given that they contrive no large fitness benefit to the individual releasing alarm cues, except perhaps in terms of indirect fitness through kin selection (Chivers et al. 2012). Since most fishes are found in mostly genetically-distinct shoals without close-kin (Krause et al. 2000; Croft et al. 2012), this reasoning appears unfounded.

Previous experience with risk can dramatically influence the way prey perceive subsequent social and predation cues. Repeated exposure to damage-released alarm cues is known to increase prey's perceived environmental risk (i.e., 'high background risk'), leading to 'high-risk' prey showing altered physiology, cognition, and behaviour (Brown et al. 2013; Ferrari et al. 2015b; Ferrari et al. 2015c; Chivers et al. 2016; Mitchell et al. 2016). This 'high-risk' behavioural phenotype can manifest over the short-term when adults are exposed over a few days (Mitchell et al. 2016), or chronically when high background risk is experienced earlier in development (Ferrari et al. 2015c). High-risk prey typically are highly neophobic (i.e., fearful of novel stimuli), irrespective of sensory modality (Brown et al. 2013; Brown et al. 2014; Brown et al. 2016; Meuthen et al. 2016; Mitchell et al. 2016), and perform worse in terms of foraging (Brown and Braithwaite 2005), spatial learning (Burns and Rodd 2008), stimulus learning, and memory retention (Brown and Braithwaite 2005; Brydges et al. 2008; Brown et al. 2014; Joyce et al. 2016). Additionally, alarm cue-induced high background risk increases the response of prey to tactile disturbances (Meuthen et al. 2016). The high-risk phenotype is likely to be adaptive in the context of environmental uncertainty, as individuals raised in high-risk environments may survive better than those from low risk environments when faced with novel predators (Ferrari 2014; Ferrari et al. 2015d). Interestingly, it remains unknown whether repeated exposures to disturbance cues can induce similar neophobic behavioural phenotypes as alarm cues, or whether background risk exposure affects prey reliance on disturbance cues.

## **1.8. Disturbance cues**

Disturbance cues have been reported in a number of vertebrate and invertebrate species in response to a simulated predator chase or other disturbing stimuli (see Table 1.1). While the

exact chemical nature and mechanism of release of disturbance cues remain unknown, a key component appears to include a pulse of nitrogenous waste, such as ammonium/ammonia in invertebrates and tadpoles (Hazlett 1985; Kiesecker et al. 1999; Manteifel et al. 2005) and urea in adult frogs and teleost fish (Munro 1957; Vavrek et al. 2008; Brown et al. 2012a). While endogenous cortisol rises in response to predation risk, there has been little support for exogenous raw cortisol as a disturbance cue (Barcellos et al. 2014; Bett et al. 2016; Henderson et al. 2017). Given the high nitrogen content of fish and amphibian urine, some authors have proposed that disturbance cues are released via pulsate urination and/or emitted from the gills in fish (Hazlett 1989; Hazlett 1990a; Kiesecker et al. 1999; Wisenden 2014). Some adult aquatic prey species are known to use urine pulses for communication purposes such as releasing mating pheromones (Stacey et al. 1986; Scott and Vermeirssen 1994). During the mating season, male fishes increase the size of their bladders significantly (Katsel et al. 1992 as cited in Sorensen and Stacey 1999) and employ urinary pulses during intrasexual competitive bouts such as while performing their opercular display (Almeida et al. 2005; Barata et al. 2007; Barata et al. 2008; Maruska and Fernald 2012; Bayani et al. 2017). If disturbance cues are, in fact, produced through urination of ammonia or urea, then they may be actively produced in the context of a predator encounter to signal predation risk to conspecifics nearby.

Chemical cues such as disturbance cues have the potential to act as an alarm signal in aquatic prey (Chivers et al. 2012; Wisenden 2014). Disturbance cues are known to increase the survival of naïve prey when presented alongside the odour of a novel predator (Mirza and Chivers 2002a), and are known to increase shoal cohesion and other cooperative antipredator behaviours (Chivers et al. 1995; Wisenden et al. 1995; Brown et al. unpublished data). However, again, disturbance cues may not always reliably indicate predation risk, and thus individuals may simply scale antipredator responses according to the relative risk they represent in their environment, as predicted by the threat sensitivity hypothesis (Helfman 1989; Vavrek and Brown 2009; Lucon Xiccato et al. 2016). Indeed, prey scale their antipredator responses according to the number of disturbance cue emitters and the concentration of disturbance cue detected (Vavrek and Brown 2009). However, it is unknown whether they also scale their responses in response to disturbance cues from more reliable individuals, such as their familiar shoalmates, or whether receivers exhibit kin-biased responses to disturbance cues. Additionally, it is unknown how the



relative predation risk experienced by prey affects their reliance on disturbance cues, such as how they release and respond to disturbance cues.

**Table 1.1.** Summary of studies on conspecific disturbance cue responses in aquatic prey (adapted from Bairos-Novak et al. 2017).

	<b>Common name, <i>species</i></b>	<b>Study</b>
<b>Arthropods</b>	Damselfly larvae, <i>Ischnura cervula</i>	Siepielski et al. (2016)
	Hermit crab, <i>Calcinus laevimanus</i>	Hazlett (1990b)
	Northern clearwater crayfish, <i>Orconectes propinquus</i>	Hazlett (1990a)
	Virile crayfish, <i>Oronectes virilis</i>	Hazlett (1990a)
	Rusty crayfish, <i>Orconectes rusticus</i>	Hazlett (1990a)
<b>Echinoderms</b>	Red sea urchin, <i>Strongylocentrotus franciscanus</i>	Nishizaki and Ackerman (2005)
<b>Amphibians</b>	Iberian green frog tadpole, <i>Pelophylax perezi</i>	Gonzalo et al. (2010)
	Red-legged frog tadpole, <i>Rana aurora</i>	Kiesecker et al. (1999)
	Wood frog, <i>Lithobates sylvaticus</i>	Bairos-Novak et al. (2017)
<b>Fishes</b>	Zebrafish, <i>Danio rerio</i>	Oliveira et al. (2013); Barcellos et al. (2014); Abreu et al. (2016)
	Iowa darters, <i>Etheostoma exile</i>	Wisenden et al. (1995)
	Convict cichlids, <i>Amatitlania nigrofasciata</i>	Vavrek and Brown (2009); Brown et al. (2012)
	Orange clownfish, <i>Amphiprion percula</i>	Manassa et al. (2013b)
	Nile tilapia, <i>Oreochromis niloticus</i>	Barcellos et al. (2011)
	White sea-bream, <i>Diplodus sargus</i>	Olivotto et al. (2002)
	Gulf toadfish, <i>Opsanus beta</i>	Fulton et al. (2017)
	Slimy sculpins, <i>Cottus cognatus</i>	Bryer et al. (2001)
	Brook trout, <i>Salvelinus fontinalis</i>	Mirza and Chivers (2002b)
	Rainbow trout, <i>Oncorhynchus mykiss</i>	Toa et al. (2004); Ferrari et al. (2008); Vavrek and Brown

(2009); Brown et al. (2012)

Sockeye salmon, <i>Oncorhynchus nerka</i>	Bett et al. (2016)
Small-scaled pacu, <i>Piaractus mesopotamicus</i>	Jordão and Volpato (2000)
South American catfish, <i>Rhamdia quelen</i>	Barcellos et al. (2011)
Pintado catfish, <i>Pseudoplatystoma corruscans</i>	Giaquinto and Hoffmann (2012)

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### 1.9. Wood frogs as a study species

Wood frogs (*Lithobates sylvaticus*, LeConte, 1825) are prevalent across much of Canada, inhabiting marshes and other moist areas, as well as neighbouring terrestrial areas. They get their name from their tendency to overwinter in upland forests and their overall tolerance for a more terrestrial lifestyle relative to other ranids (Howard 1980; Martof and Humphries 2017).

Wood frogs are an ideal study species for kinship comparisons because their breeding system is largely monogamous and spatially-separated ponds show little genetic overlap. Spring breeding takes place in a single week following the spring thaw. Males mount the back of females and clasp them in a grip known as an ‘amplexus’ until the female finds a suitable location to deposit her eggs, which can take anywhere from 2 hours to 3 days (Howard 1980; Berven 1981). Larger males may attempt to dislodge the amplexant males (Herreid II and Kinney 1967; Howard 1980), however, eggs are always fertilized by the amplexant male and very few males mate with multiple females in the same breeding season (Howard 1980; Howard and Kluge 1985), likely due to the low probability of males finding a second mate and dislodging the amplexant male within the short breeding interval of 4-9 days (Herreid II and Kinney 1967; Howard 1980). Population genetics analyses reveal that wood frogs are highly philopatric during the breeding season, with 82% of juveniles returning to their natal ponds to breed and nearly all adults returning to the same pond year after year (Berven and Grudzien 1990). This means that genetic relatedness of frogs breeding at the same ponds is high and likely distinct from frogs of

spatially-separated ponds. The egg deposition strategy of female wood frogs allows for easy collection of newborns from the same parents and without much risk of shared paternity.

Wood frogs are somewhat unique in that they select ephemeral ponds to lay their eggs that eventually dry up over the course of the summer, presumably because these ponds lack permanent aquatic predators (Howard 1980). Females lay all their eggs in distinct egg masses or clutches in shallow, open areas with emergent vegetation (Howard 1980; Seale 1982), as development is largely dependent on water temperatures and thus insolation (Herreid II and Kinney 1967). Female wood frogs often select the same egg oviposition sites as other females that have previously laid within the same pond (Howard 1980; Berven 1981) and egg masses typically consist of ~700 eggs (up to 3000) of 1.6 mm diameter (Herreid II and Kinney 1967). Wood frog tadpoles typically hatch in a couple of weeks or less and immediately face many invertebrate predators lying in wait to ambush them, such as predaceous diving beetle larvae (f. Dytiscidae) (Ferrari et al. 2015a). Tadpoles therefore must quickly learn their highly variable local pond environments after hatching. Often this is accomplished through tadpoles associating conspecific alarm cues with the odour of a novel predator and then reducing their overall activity to the predator odour in subsequent encounters (Chivers and Ferrari 2013). This association can even occur during embryonic development in some species (Mathis et al. 2008; Supekar and Gramapurohit 2017). Similar associative learning of novel predators can also occur with disturbance cues in Iberian green frog tadpoles (*Pelophylax perezi*), although it is thought to be a weaker association (Ferrari et al. 2008; Gonzalo et al. 2010). As tadpoles continue to develop their limb buds and eventually fore- and hindlimbs (stages 26+; Gosner 1960), they fail to respond to chemical cues indicative of risk (Ferrari, unpublished). Tadpoles typically metamorphose into juvenile frogs within 50–120 days after hatching, depending on temperatures and water levels (Herreid II and Kinney 1967; Berven 1981).

Wood frog tadpoles are also known to recognize and associate more with kin, and differentiate kin even when they have no prior (post-hatching) experience with their siblings (Cornell et al. 1989). Indeed, wood frog tadpoles likely use self-referent phenotype matching as a kin recognition mechanism (Waldman 1984; Cornell et al. 1989; Gamboa et al. 1991). For instance, wood frog tadpoles reared in mixed cohorts still can recognize and preferentially associate with true siblings over familiar non-siblings after hatching (Waldman 1984).

## 1.10. Research objectives

A few studies have manipulated disturbance cues released and received by prey, such as the number of cue emitters and the concentration of cue detected (e.g., Vavrek and Brown 2009), the background level of urea/ammonia (e.g., Vavrek et al. 2008; Brown et al. 2012b), and the nature of disturbance used to obtain the cue in the first place (e.g., Abreu et al. 2016). Yet, few studies have examined whether disturbance cues from familiar or genetically-related individuals evoke different antipredator responses in receivers, or how disturbance cues are differently produced and responded to when prey come from high- vs. low-predation risk environments. Thus, my main objective was to assess whether prey respond more on disturbance cues released by different – and potentially more reliable – individuals. More specifically, I explored three main questions:

*How do receivers respond to disturbance cues produced by familiar individuals relative to cues produced by individuals with whom they had no experience?* In Chapter 2, I looked at the behaviour of tadpoles that received disturbance cues produced by tadpoles that were familiar or unfamiliar to the test subject to address this question.

*How do receivers respond to disturbance cues produced by closely-related kin compared to cues produced by non-kin?* In Chapter 3, I separated siblings from the same clutch prior to egg hatching, then later exposed some individuals to disturbance cues from their unfamiliar siblings or to disturbance cues from unfamiliar tadpoles born from different egg clutches, and examined whether close-kin disturbance cues would provoke a stronger response relative to likely non-kin disturbance cues. I also examined this same question in terms of responses to conspecific alarm cues from kin and non-kin.

*How does past predation risk experience affect the production of and response to disturbance cues?* In Chapter 4, I exposed tadpoles repeatedly to chemical alarm cues over several days to induce a high-risk phenotype, or exposed them to a water control. I then examined the release of disturbance cues from groups of unfamiliar tadpoles from either the high-risk or low-risk disturbance cue treatments, and observed the responses of high- and low-risk background tadpoles.

### **1.11. Anticipated significance**

While many animal behaviourists would feel that the study of prey communication is intrinsically and fundamentally enthralling, there are also many human- and ecosystem-centric applications of disturbance cues. For instance, disturbance cues may represent an entirely novel animal signalling system that could impact how we manage all aquatic species, and may yield practical applications in terms of aquatic prey reintroductions and conservation. For example, young-of-year survival may be increased through conditioning antipredator responses to natural predators by exposing them to predator odour paired with alarm cues (Rehnberg and Schreck 1987; Brown and Godin 1997; Crane and Mathis 2011). This type of research may have important implications for the conservation of amphibians, species that have seen increasingly high mortality in the wild due to competition and predation by invasive species, disease, and low breeding success in captivity (Dodd Jr. and Seigel 1991; Kats and Ferrer 2003; Murphy and Gratwicke 2017).

## **Chapter 2: Tadpoles respond to disturbance cues from strangers but not familiar individuals**

### **2.1. Introduction**

Familiarity, and presumably cooperation, yields important benefits to aquatic prey antipredator responses. For example, predator inspection behaviour is known to increase prey survival via predator recognition (Brown and Godin 1999), predator deterrence (Godin and Davis 1995), and/or by producing a visual signal that highlights the threat nearby to other prey (Smith and Smith 1989). When shoals are composed of reliably-cooperating individuals and, unsurprisingly, familiar rather than unfamiliar shoalmates, predator inspections become more frequent (Milinski 1987; Milinski et al. 1990; Chivers et al. 1995). Shoal cohesion (reducing the distance among shoaling prey) is another viable strategy for avoiding predation (Mathis and Smith 1993) and this also increases in shoals consisting of familiar or related individuals (Chivers et al. 1995; Höjesjö et al. 1998; Hain and Neff 2009; Atton et al. 2014). As a result, familiar shoals in general may simply respond more rapidly to predator attacks compared to unfamiliar shoals (Griffiths et al. 2004), and they may be less reactive to false predator stimuli (Wolcott et al. 2017).

In aquatic prey such as freshwater fishes and tadpoles, unique chemical signatures are likely the predominant sensory modality used when fish recognize familiar conspecifics; yet, visual and auditory cues may also be used. Fathead minnows (*Pimephales promelas*) appear to separate familiar individuals from unfamiliar using only chemical cues (Brown and Smith 1994), and there are many examples of fishes and tadpoles using chemical cues over visual ones to preferentially associate with familiar individuals (Van Havre and FitzGerald 1988; Blaustein and Waldman 1992; Krause et al. 2000). Aquatic prey also use their olfaction when assessing risk in their environments, with chemical alarm cues, disturbance cues, or learned predator odours being important (Ferrari et al. 2010). Yet, few studies to date have examined how familiarity among

aquatic prey affects their reliance on conspecific cues indicating risk. In this chapter, I allowed wood frog tadpoles to familiarize over the course of one month in the same tank then assessed their antipredator responses to either disturbance cues or undisturbed cues (as a control) from familiar or unfamiliar prey. Given that prey are more likely to engage in coordinated antipredator behaviours such as predator inspections or tighter shoaling when familiar with one another, I hypothesized that tadpoles would respond more strongly to disturbance cues taken from groups of familiar conspecifics compared to disturbance cues from unfamiliar conspecifics.

## **2.2. Methods**

### *2.2.1. Study species*

I collected 18 distinct, large egg clutches from three different ephemeral ponds northwest of Saskatoon between April 28<sup>th</sup> and May 3<sup>rd</sup>, 2017 and stored them outdoors at the University of Saskatchewan (Saskatoon, SK, Canada). The natural ponds where tadpoles were collected are known to have no fish predators, but do experience invertebrate, salamander, and avian predation. Each egg mass was stored individually in 50-l outdoor pools filled with at least day-old filtered and dechlorinated water and covered with a light mesh to prevent avian predation. Tadpoles hatched within a fortnight of collection and fed on naturally-growing algae on the walls of their outdoor pools. I conducted ~10% water changes every day and all tanks and experiments were conducted outdoors.

### *2.2.2. Familiarization and Cue Preparation*

To ensure familiarity but limit kin association, I placed distinctly larger and smaller tadpoles that were each from different egg clutches into a 7 l glass tank (familiarization tank) filled with 2 l of filtered water with a mesh covering. There were 15 familiarization tanks, each with 8 larger individuals collected from the same 4/18 distinct egg clutches in addition to 17 smaller tadpoles taken from the remaining 14/18 egg clutches. This was done to ensure that there were no common kin between the two differently sized groups, so that when disturbance cues were prepared from the larger individuals, the smaller individuals receiving the cues would always be non-siblings with the cue donors. Hence, these 25 tadpoles were raised together over a period of 32-33 days to allow tadpoles to become familiar with one another and shared the same number of individuals from each pond and egg mass collected. I conducted water changes every

second day to maintain tank water quality and provide a form of disturbance that tadpoles could react to. After the familiarization period, I removed the 6-8 distinctly larger individuals from each tank group (3/15 tanks had some mortality of larger tadpoles) to prepare undisturbed and disturbance cues. Cue donors were rinsed and placed them in a 0.5-l plastic cup filled with water at a dilution level of 20 mL of water per tadpole. This final cue concentration (i.e., 0.05 tadpoles/ml) is similar to previous studies using disturbance cues (e.g., Gonzalo et al. 2010).

All donor tadpoles were left undisturbed for an hour in order to acclimate. After the acclimation period, approximately 0.5-l of fresh filtered water was simultaneously added and removed from cups via gravity-fed airline hoses, thus cups maintained an approximately the same water volume throughout the water change. While this was occurring, I was careful to remain out of sight and as quiet as possible to minimize disturbance. Donor tadpoles were left undisturbed in the cups for 10 minutes thereafter, upon which time I used the same airline hose system to obtain 60 ml of undisturbed cue and added back 60 ml of fresh filtered water.

Immediately following the collection of undisturbed cues, I used two identical glass rods with black opaque plastic ends to simulate a predator chase in each cup. I conducted paired chases simultaneously on two different donor groups by mirroring all movements on one side with the same on the other side while taking care to avoid physical contact with tadpoles in either cup. I used cues from donor groups chased in the same pair to create the familiar vs. unfamiliar cue treatments. Thus, cues coming from familiar and unfamiliar individuals had very similar chase events that were completely mirrored and that had occurred simultaneously. Both groups were left undisturbed for a minute following the disturbance to ensure tadpoles had enough time to produce disturbance cues, then 60 ml of disturbance cues were collected using the airhose system.

All cups, airline tubes, and glass rods used in the chase simulation were subsequently washed thoroughly after the cue extraction. Each tadpole was used only once for cue production and subsequently removed from the experiment (they were not tested as receivers). Cues were produced from all the larger individuals from all of the familiarization tanks ( $k = 15$ ), and were used within 2 h of being produced.



### *2.2.3. Testing Protocol*

Tadpoles are known to decrease activity in response to nearby predation risk (Hokit and Blaustein 1995; Kiesecker and Blaustein 1998; Chivers and Mirza 2001). Gosner (1960) stage 25 tadpoles from each familiarization tank were randomly allocated to their own 0.5-l plastic cups filled with ~0.4 l of filtered water and allowed to acclimate for at least an hour prior to testing. Tadpole activity was assessed using the number of times the tadpole crosses the medial line of the cup during a 4-minute pre-exposure and a 4-minute post-exposure period (Ferrari and Chivers 2010; Gonzalo et al. 2010). After the 4-minute pre-exposure period, 5 ml of either undisturbed or disturbance cues from either the same familiarization tank (familiar cues) or from the different familiarization tank (unfamiliar cues) were slowly dripped into each cup. Tadpoles were then observed for 4-minutes post-exposure to assess the relative change in activity caused by cue injection. To ensure a decrease in activity could be observed, should such a decrease occur, I only tested tadpoles that were active (with >7 lines crossed) in the pre-exposure period, otherwise I waited until tadpoles began actively moving again. The order of treatments was randomized and I was blind to the cues used in testing tadpoles. I measured the total body length of each donor and receiver tadpole after testing. The antipredator response of freezing in tadpoles dwindles with the size and age of the receiver, with tadpoles eventually responding to fearful stimuli with increased activity (e.g., >30 mm in wood frogs; Gallie et al. 2001; Fraker 2008). Additionally, tadpoles are opportunistic cannibals as they get larger, consuming conspecifics when they are much larger than them (Faragher and Jaeger 1998; Jefferson et al. 2014). Little mortality was observed in my tanks, likely because of the abundant algal food supply coating the sides of each tank.

### *2.2.4. Statistical Analysis*

Initially, the data appeared to have a number of outliers and was not normally distributed. Due to the relatively large size of some of the tadpoles at the time of testing, I decided to remove tadpoles from the analysis that were >30 mm in body length (3.4% of all data). I also removed overly active tadpoles with >40 line crosses over a 4-min period from the final analysis (2.7% of all data) due to their disproportionately large impact when analyzing absolute differences in line crosses (i.e., post – pre line crosses). Finally, I used old cue (>2 hours old) for four of the trials (2.7% of all data) and so these cases were excluded from the analysis. Upon removing these

trials (8.8% of all data), model residuals were much closer to being normally distributed and all other parametric assumptions were satisfied.

I interpreted significance of models using a critical  $\alpha = 0.05$  and all tests were two-tailed and implemented using *R* v.3.3.2 (R Development Core Team 2016). Linear mixed-effects models were fit using package *lme4* (Bates et al. 2015) and plots were created using the *ggplot2* package (Wickham 2009).

In order to use absolute differences in lines crossed (post – pre), pre-exposure line crosses must be compared among treatment groups. These were compared in a mixed model with fixed effects of familiarity type (familiar or unfamiliar), cue type (undisturbed or disturbance cue), their interaction, and a covariate of total length of the receiver tadpole ( $C_{size}$ ), as well as a random effect ( $Z$ ) of the specific donor group ( $Y_{pre\ lines} \sim X_{familiarity} \times X_{cue\ type} + C_{size} + Z$ ). I included the covariate of size and the random effect in the final model only if their estimates were significantly different from zero, otherwise the model was simplified by dropping non-significant terms. After modelling pre-exposure line crosses, I used a similar initial model for modelling the difference in line crosses ( $Y_{diff\ lines} \sim X_{familiarity} \times X_{cue\ type} + C_{size} + Z$ ) and dropped non-significant terms to obtain a more parsimonious model.

Significant interactions among fixed effects were examined by splitting the data by each factor. To account for the increased likelihood of committing a type I error, I use a critical  $\alpha' = \alpha/(\# \text{ splits})$  for significance interpretations.

To test if the variance of the random effect term significantly differed from zero (and thus determine if the random effect of donor group need be included), I use a restricted likelihood ratio test implementing extremely rapid and relatively powerful spectral decomposition algorithm of Crainiceanu and Ruppert (2004) for obtaining a simulated finite sampling distribution of a single random effect, as implemented in *R* with package *RLRsim* (Scheipl et al. 2008). This method circumvents the infamous ‘boundary problem’ plaguing mixed effect models. If the likelihood ratio test (LRT) failed to reject the null hypothesis that the variance of the random effect term differs from zero, I used a general linear model instead of a linear mixed effects model.

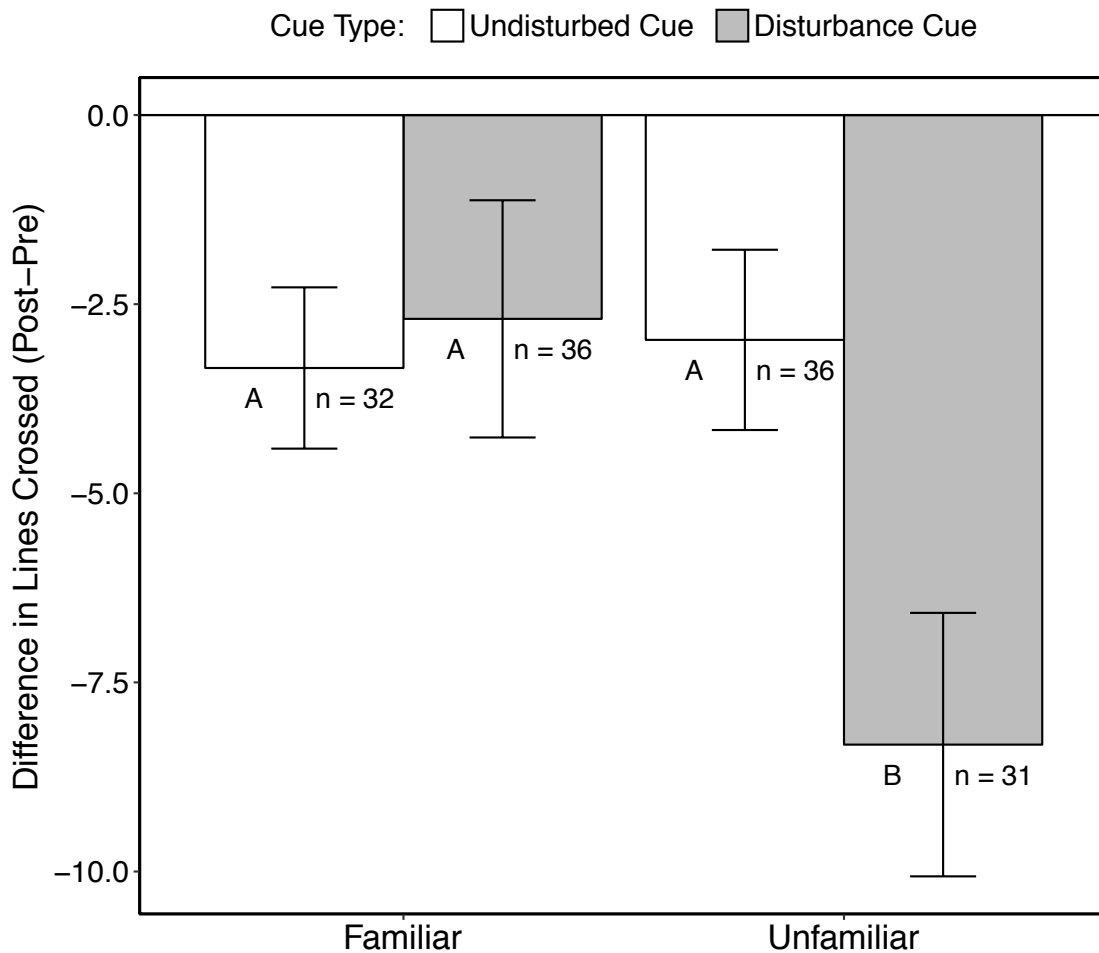
### 2.3. Results

The mean length of donors after the one-month familiarization period was  $39.3 \pm 3.8$  mm (mean  $\pm$  SD) and most were past Gosner stage 25, reaching up to stage 40 with full forelimbs and hindlimbs. Receivers were  $24.5 \pm 2.4$  mm long (mean  $\pm$  SD). Receiver sizes did not differ among treatment groups (2-way ANOVA, overall  $F_{3,131} = 1.57$ ,  $P = 0.2$ ,  $N = 135$ ).

Pre-exposure line crosses did not differ across treatment groups. For the pre-exposure number of line crosses model ( $Y_{pre\ lines} \sim X_{familiarity} \times X_{cue\ type} + C_{size} + Z$ ), donor group was an important random effect to include (simulated finite sample distribution of  $Z$ :  $LRT = 7.40$ ,  $P = 0.0013$ ), but there were no significant fixed effects thereafter (linear mixed effects model, all  $F_{1,116} \leq 1.67$ ,  $P \geq 0.20$ ,  $N = 135$ ), indicating equivalent pre-cue exposure line crosses among the different treatments and irrespective of receiver size. Therefore, I was able to use the absolute difference in lines crossed instead of the percent difference measure for further analyses. The mean  $\pm$  SE pre-exposure line crosses was  $14.0 \pm 0.57$  lines.

Tadpoles decreased their line crosses most when exposed to disturbance cues taken from unfamiliar donors (Fig. 2.1). I used a similar initial model to analyze the difference in lines crossed ( $Y_{diff\ lines} \sim X_{familiarity} \times X_{cue\ type} + C_{size} + Z$ ). The random effect of donor for the change in lines crossed had a variance that was not significantly different from zero ( $Z$ :  $LRT = 0$ ,  $P = 0.38$ ) and the receiver size covariate had no effect on tadpole responses (multiple regression term for  $C_{size}$ :  $F_{1,130} = 0.04$ ,  $P = 0.85$ ,  $N = 135$ ), so I simplified the model to a two-way ANOVA ( $Y_{diff\ lines} \sim X_{familiarity} \times X_{cue\ type}$ ). This new model had a significant interaction among cue type and familiarity ( $F_{1,131} = 4.48$ ,  $N = 135$ ,  $P = 0.036$ ) and so was split by each of the two factors to determine the shape of this interaction and a critical  $\alpha' = 0.025$  was used.

Interestingly, tadpoles responded much more to disturbance cues from unfamiliar individuals relative to familiar individuals (Fig. 2.1; two-sample t-test,  $t_{65} = 2.41$ ,  $P = 0.019$ ,  $n = 67$ ,  $\alpha' = 0.025$ ), and disturbance cues from unfamiliar donors elicited more of a response relative to undisturbed cues from unfamiliar donors (Fig. 2.1;  $t_{65} = 2.59$ ,  $P = 0.012$ ,  $\alpha' = 0.025$ ,  $n = 67$ ). On the other hand, disturbance cues from familiar individuals elicited no response relative to the undisturbed cues of the familiar individuals (Fig. 2.1;  $t_{66} = 0.33$ ,  $P = 0.74$ ,  $n = 68$ ). There were no significant differences in responses to familiar vs. unfamiliar undisturbed cues (Fig. 2.1;  $t_{66} = 0.23$ ,  $P = 0.82$ ,  $n = 68$ ).



**Fig. 2.1.** Mean change ( $\pm$  SE) in lines crossed by wood frog tadpoles from pre- to post-cue exposure in response to two different types of cues (undisturbed or disturbance cues) from familiar (raised together for 32-33 days) or unfamiliar conspecifics. Different letters indicate statistical differences at  $\alpha = 0.05$  and sample size is indicated per bar.

## 2.4. Discussion

Contrary to my initial predictions, tadpoles ignored all undisturbed cues and disturbance cues released by 1-month familiar and unrelated conspecifics, but did respond to the disturbance cues produced by unrelated strangers. Tadpoles responding to disturbance cues from unfamiliar individuals decreased their relative line crossing by 52.8%, but did not respond to disturbance cues from familiar individuals nor the control cues (~22.3% decrease overall). This is interesting, since the exact same cues were given to both familiar and unfamiliar individuals, so the difference cannot be explained by differences in cue production. During the familiarization

period, tadpoles could see outside their tanks and may have been repeatedly frightened as I walked by them. Thus, one explanation for the observed results may be that familiar individuals learned to ignore disturbance cues from familiar individuals because they were not reliably paired with risk, resulting in prey habituation to familiar disturbance cues. Recall Aesop's tale of *The Shepherd Boy and the Wolf* (Wetherell 1926), in which a boy continues to 'cry wolf' unreliably to nearby villagers until his message is ignored. Indeed, many species seem to ignore conspecific alarm calls that have been made unreliable through repeated playbacks (Cheney and Seyfarth 1988; Bliss 1995; Hare and Atkins 2001; Blumstein et al. 2004). Further experiments that manipulate cue reliability are required in order to confirm if this was indeed occurring.

Other possible explanations include increased activity or decreased stress as a result of sensing familiar conspecific cues. Many familiarity studies involve increased shoaling activity as a result of sensing familiar chemical cues (Brown and Smith 1994; Griffiths and Magurran 1999a), and so familiar cues could increase the overall activity of receivers, which, in turn may negate large decreases in activity expected upon receipt of disturbance cues. However, if this was occurring, one would expect increased activity in tadpoles receiving familiar undisturbed cues, or at least increased activity relative to those receiving unfamiliar undisturbed cues; yet, this is not the case. Another possible explanation could be that in some species, prey experience less stress and are less responsive to threatening stimuli when they sense familiar individuals present nearby. For example, Japanese black heifers (*Bos primigenius*) are less stressed when in a group with familiars relative to groups composed of unfamiliar individuals (Takeda et al. 2003), and guppies in familiar groups were less responsive to a visual predator stimulus compared to unfamiliar groups of guppies (Wolcott et al. 2017). In this scenario, tadpoles from the familiar treatments would have responded less to familiar cues (such as disturbance cues) as a result of them perceiving familiar individuals nearby and causing decreased stress via social buffering (Smith and Wang 2014). However, again, undisturbed cues from familiar individuals would then be predicted to evoke a lower response compared to undisturbed cues from unfamiliar individuals, if this were the case.

This experiment provides evidence of wood frog tadpoles either differentiating among reliable vs. unreliable cues/individuals, or discriminating familiar vs. unfamiliar cues/individuals. To determine if prey remember one another based on their past reliability, one would have to directly manipulate the reliability of cues from different individuals, as well as the risk present

after reception of the manipulated cues. For instance, individuals could be made reliable or unreliable by pairing the injection of their disturbance cues with an immediate predation threat (e.g., a simulated predator chase), or without a threat thereafter. This could also be done with two distinct disturbance cues (one made reliable and one made unreliable) on the same receiver group. If receivers responded to the reliable disturbance cues while ignoring the unreliable cues, this would be evidence of individuals discriminating cue reliability. Theoretical models predict that receivers should discriminate senders as reliable vs. unreliable more when the costs of ignoring a dishonest signal are higher and the benefits of an honest signal are lower (Koops 2004). In other words, when the cost of ignoring a ‘false’ disturbance cue is energetically costly to the organism (due to reduced time available for other activities such as foraging), while the benefits of responding to a ‘true’ disturbance cue are minimal. The latter is simply not the case in the context of predation, given the immediate and large fitness costs of being killed. Instead of cue reliability, it may be just as easy for prey to distinguish between familiar vs. unfamiliar individuals, and respond proportionally to their honest experience with the respective cues from each category. To test if this were true, receivers could be given disturbance cues from other previously familiar individuals to determine if they respond similarly to all cues arising from ‘familiar’ individuals. In either case, more experiments need to be done to better understand how aquatic prey classify and conceptualize reliable vs. unreliable information, as has been done in studies of reliability assessment in sciurids and vervet monkeys (Cheney and Seyfarth 1988; Hare and Atkins 2001; Blumstein et al. 2004).

## **Chapter 3: Kinship does not affect tadpole responses to disturbance or alarm cues**

### **3.1. Introduction**

Many species use odour or chemical cues to differentiate familiar from unfamiliar and kin from non-kin (see Griffiths 2003 for a review). While many mammals and aquatic animals predominantly rely on chemoreception for differentiating kin from non-kin (e.g., Mehlis et al. 2008; Mateo 2017), some birds may also discriminate kin via odours, as seen in stormpetrels and penguins (Coffin et al. 2011; Bonadonna and Sanz-Aguilar 2012). Even in early life stages, such as with anuran tadpoles, individuals can recognize kin and preferentially associate with these individuals (see Blaustein and Waldman 1992 for a review). Yet, in an antipredator context, kin-biased behaviours are not well studied. Sherman (1981, 1985) noted kin-biased alarm calling and association preferences among kin, with mothers calling more than other adults without offspring. In aquatic species such as tadpoles, kin recognition allows cannibalistic-morph tadpoles to consume predominantly non-kin, thus removing potential competitors (Pfennig et al. 1993). Other cooperative antipredator behaviours such as shoal cohesion and predator inspections are bolstered in aquatic species grouped with close-kin relative to non-kin shoals (Hain and Neff 2009; Hesse et al. 2015).

Despite the commonality and apparent benefits of kin-biased association preferences, little is known regarding prey preferentially responding to cues produced by closely-related conspecifics relative to cues from non-kin. Meuthen et al. (2014) found that alarm cues produced by kin and non-kin are perceived similarly in the cichlid *Pelvicachromis taeniatus*. Hare and Murie (1996) also found no difference in the responses of juvenile Richardson's ground squirrels to alarm calls from related individuals. Herein, I hypothesized that wood frog tadpoles respond to cues from their siblings and non-siblings differently, and predicted that they would respond more to disturbance cues and alarm cues from their own siblings compared to cues produced by

individuals from different egg clutches, while controlling for the effect of familiarity. If receivers respond preferentially to disturbance cues from their immediate siblings, this would suggest that disturbance cues are maintained via kin selection.

## **3.2. Methods**

### *3.2.1. Tadpole collection and kinship*

I collected distinct, large egg clutches from ephemeral ponds northwest of Saskatoon between April 28<sup>th</sup> and May 3<sup>rd</sup>, 2017. Each egg clutch was split into two and raised in separate large pools to make sure that some of the tadpoles from each clutch were not familiar with one another. Some of the egg clutches were collected from the same pond, while some were collected from two other similar ponds >7 km away.

Distinct wood frog egg clusters taken from the same pond are more likely to be genetically similar relative to egg clusters from different, spatially-separated ponds (see 1.10; Berven and Grudzien 1990). On the other hand, egg clusters from different ponds face entirely different environmental conditions during embryonic development, and tadpoles may respond differently to cues produced by tadpoles raised in distinct environments. Lucon-Xiccato et al. (2016) demonstrated that the antipredator response of tadpoles to alarm cues depends on whether the alarm cue donors were raised in a low- vs. high-risk environment. Additionally, in Chapter 4, I demonstrate that background risk affects the production and response to disturbance cues. Thus, I exposed receivers to unfamiliar cues produced by tadpoles from the same clutch, tadpoles from a different clutch taken from the same pond, and tadpoles from a different clutch collected from a different pond. If tadpoles from the same pond are more similar genetically relative to tadpoles from a different pond, then the response to disturbance cues produced by tadpoles from a different clutch in the same vs. different ponds may differ. Similarly, if tadpoles from different ponds produce different cues due to their egg deposition environment, I again expect the responses of receiver tadpoles to cues produced by tadpoles from a different clutch in the same vs. different ponds to differ. Thus, the two different clutch comparisons relative to the same-clutch cues serve as a litmus test of possible underlying genetic and/or environmental confounds in this experiment. All cues used in the experiment were unfamiliar to receivers, save for possible embryonic experience of same-clutch cues prior to egg collection, which is not easily avoided.



### 3.2.2. Cue preparation and testing

Cues were prepared in a way identical to that outlined in the methods section 2.2.2, with the exception of alarm cues. After obtaining undisturbed cues and disturbance cues from the same 10 individuals, they were rinsed and euthanized via a blow to the head (using a mortar and pestle). Their bodies were emulsified, the resulting solution mixed with 200 ml of filtered water, and filtered through cotton gauze to remove any large pieces of tissue that remained (Ferrari et al. 2007; Ferrari and Chivers 2010). All cues were released at similar ecologically-relevant concentrations by using the same number of individuals in the same volume of water.

Testing immediately followed cue preparation and used an identical protocol as testing in Chapter 2. I required tadpoles to be less than 30 mm long for testing, have at least 7 pre-exposure line crosses, and I used cues within 2 hours of preparation to avoid potential cue expiry. The order of treatments was randomized and I was blind to both the cue type and kin group of tadpoles being tested. Finally, to compare to the undisturbed cue I used as a control, I had a limited number of trials examining the responses of tadpoles to filtered water without tadpoles present.

### 3.2.3. Statistical analysis

Due to cloudy and windy weather causing a great disturbance following cue exposure, 5.05% of trials were removed. Linear models were implemented using *R* v.3.3.2 (R Development Core Team 2016). Linear mixed-effects models were fit using package *lme4* (Bates et al. 2015) and plots were created using the *ggplot2* package (Wickham 2009). Similar to previously, I used the absolute difference in lines crossed (post – pre) after comparing pre-exposure line crosses among the different treatment groups.

Initial linear mixed models for both pre-exposure line crosses and for absolute differences initially included the effects of clutch comparison (kin, non-kin same population, or non-kin different population), cue type (undisturbed cue, disturbance cue, or alarm cue), their interaction, and a random effect ( $Z$ ) of donor group (i.e., a linear mixed model of  $Y \sim X_{clutch\ comparison} \times X_{cue\ type} + Z$ ). As previously, I compared these models with a linear model lacking the random effect term using the simulated finite sample distribution method discussed previously (see section 2.2.4; Crainiceanu and Ruppert 2004; Scheipl et al. 2008). Models were simplified from the initial model by dropping non-significant terms to obtain a more parsimonious final model.

Finally, I compared tadpole responses to undisturbed cues from the same clutch and filtered water using an independent samples t-test. I interpreted significance using a critical  $\alpha = 0.05$ , all tests were two-tailed, and all parametric assumptions of linear models were satisfied.

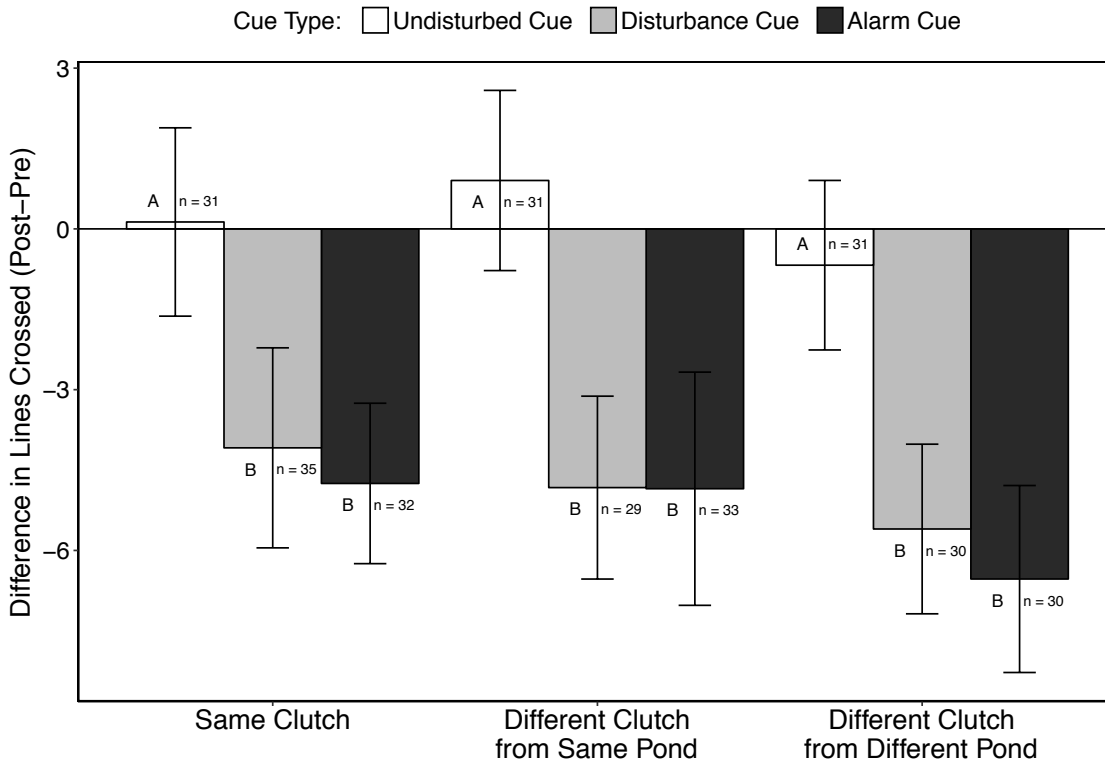
### 3.3. Results

The mean length of the 60 donors was  $24.2 \pm 3.52$  mm (mean  $\pm$  SD). I did not record the length of each receiver for this experiment, but I recorded a mean length of 23 mm in a subset of receivers ( $n = 40$ ), with lengths ranging between 18–29 mm long.

#### 3.3.1. Clutch comparison $\times$ cue

Pre-exposure line crosses were similar across all treatment combinations. In the initial mixed model of pre-cue exposure line crosses, the variance of the donor group term did not differ from zero (simulated finite sample distribution of  $Z$ : LRT = 0,  $P = 0.34$ ), and none of the effects were significant in the reduced two-way ANOVA (overall  $F_{8,273} = 0.42$ ,  $P = 0.91$ ). Thus I proceeded to use absolute difference from pre- to post-cue exposure in line crosses to assess the antipredator response of tadpoles to different cues. The mean  $\pm$  SE pre-exposure line crosses was  $18.6 \pm 0.58$  lines.

Tadpoles decreased their line crosses to disturbance cues and alarm cues, but there were no differences among the three clutch comparisons (Fig. 3.1). The initial mixed model of absolute difference in line crosses ( $Y_{diff\ lines} \sim X_{clutch\ comparison} \times X_{cue\ type} + Z$ ) yielded a random effect variance that did not differ from zero ( $Z$ : LRT = 0,  $P = 0.33$ ), and so the model was simplified to a two-way ANOVA (overall  $F_{8,273} = 2.37$ ,  $P = 0.018$ ,  $N = 282$ ). The interaction between cue type and clutch comparison was not significant ( $F_{4,273} = 0.06$ ,  $P = 0.99$ ,  $N = 282$ ). The cue that tadpoles were exposed to significantly affected the difference in lines crossed ( $F_{2,273} = 8.87$ ,  $P = 0.0002$ ,  $N = 282$ ), but the clutch comparison factor had no effect ( $F_{2,273} = 0.59$ ,  $P = 0.56$ ,  $N = 282$ ). Specifically, disturbance cues and alarm cues significantly decreased line crosses from pre- to post-exposure relative to undisturbed cues (undisturbed vs. disturbance cue:  $t_{185} = 3.55$ ,  $P = 0.0005$ ,  $n = 187$ ; undisturbed vs. alarm cue:  $t_{186} = 3.83$ ,  $P = 0.0002$ ,  $n = 188$ ), and the two did not differ from one another (disturbance vs. alarm cue:  $t_{187} = 0.38$ ,  $P = 0.71$ ,  $n = 189$ ).



**Fig. 3.1.** Mean change ( $\pm$  SE) in lines crossed by wood frog tadpoles from pre- to post-cue exposure in response to three different types of cues (undisturbed, disturbance, or alarm cue) from unfamiliar conspecifics raised either from the same egg clutch (kin), a different egg clutch in the same pond (non-kin same population), or a different egg clutch found in a separate pond several kilometres away (non-kin different population). Different letters indicate statistical differences at  $\alpha = 0.05$  and sample size is indicated per bar.

### 3.3.2. Control cues

I compared the responses of tadpoles to undisturbed cues from kin donors vs. the response to filtered water alone ( $Y_{diff\ lines} \sim X_{cue\ type}$ ) and found no difference (Student's t-test,  $t_{49} = 0.67, P = 0.50$ ).

## 3.4. Discussion

Tadpoles responded similarly to cues across all clutch comparisons, regardless of whether tadpoles were from the same or different clutches (Fig. 3.1). The reduction in activity resulting from disturbance cues and alarm cues collected from the same individuals was also similar, and significantly more pronounced relative to the undisturbed cues. Specifically, tadpoles decreased

their relative line crosses by 26.0% and by 27.5% in response to disturbance cues and alarm cues, respectively, whereas they increased their line crosses by 0.7% in response to undisturbed cues. The similar response to kin vs. non-kin alarm cues has been observed previously. For example, Meuthen et al. (2014) found no difference in the response of cichlids to kin vs. non-kin alarm cue and Richardson's ground squirrels respond similarly to alarm calls emitted by kin vs. non-kin, including calls from their own mothers (Hare and Warkentin 2012). It is unlikely that prey would preferentially respond to cues or signals when they are just as likely to be reliable when they are emitted, since they likely make the emitter more conspicuous to predators and are therefore costly to produce (Maynard Smith 1965).

There are many explanations as to why tadpoles did not respond differently to disturbance cues produced by closely-related siblings relative to non-siblings from the same or different ponds. It is possible that the difference between receiver responses to kin vs. non-kin cues is so nuanced and slight that my study could not detect the difference, or the cues used in the experiment were too potent/concentrated to detect differences in the response of tadpoles. Unlike the familiarity experiment in Chapter 2, tadpoles in this experiment were raised in large pools of >100 tadpoles from the same egg clutch prior to being tested with unfamiliar cues. Some studies have suggested that the effects of familiarity and kinship are only seen in smaller group sizes and otherwise dwindling in larger groups due to cognitive and/or energetic constraints (Griffiths and Magurran 1997a; Schweitzer et al. 2011). This is a common difference between laboratory and field experiments, as in the field, individuals may be in much larger groups and infrequently come across familiar and/or closely-related individuals (Griffiths 2003). Thus, the ability to differentiate kin from non-kin could arise ontogenetically in tadpoles, depending on the group size most commonly experienced by tadpoles early on in life. This also would explain why I observed differences dependent on familiarity and not kinship. Another confound that obfuscates comparisons between the two experiments is that in the familiarity experiment, tadpoles were much larger and often at later stages of development relative to the kinship experiment. In either case, it is interesting to note that sample sizes were roughly similar between the two experiments, suggesting that the kinship experiment had enough statistical power to reveal differences among clutch comparisons.

Familiarity and/or cue reliability may supersede kinship effects in tadpoles and other aquatic prey. Familiarity is more commonly used among group-living species (Krause et al.

2000; Griffiths 2003), and prey may prefer associating with familiar conspecifics rather than kin or avoid kin in order to avoid potential inbreeding (Hare and Murie 1996; Gerlach and Lysiak 2006; Coffin et al. 2011; Bonadonna and Sanz-Aguilar 2012; Croft et al. 2012). Possibly, familiarity may act as a placeholder for wood frog tadpole kin recognition mechanisms, present earlier in development until phenotype matching is more attuned later on in life. Such appears to be the case in newborn Columbian ground squirrels, who use familiarity in their first 30 days of life, then switching to phenotypic matching thereafter (Mateo 2010; Mateo 2017). Finally, familiarity may be a requirement for kin-biased behaviour, as it is in guppies (Griffiths and Magurran 1999a). Moreover, all these hypotheses disregard the fact that many studies have found early-stage wood frog tadpoles (2-6 weeks old) preferentially associate with unfamiliar siblings over non-siblings, regardless of past experience (Cornell et al. 1989; Gamboa et al. 1991); so, it is unlikely that the tadpoles in my experiment relied more on familiarity, or failed to differentiate kin.

It is also possible that tadpoles did not respond to disturbance cues from differently-related individuals because they respond similarly to disturbance cues from even partially-related individuals. For example, Hoogland (1986) observed that amicable behaviour in black-tailed prairie dogs was similarly directed to any related individual, regardless of how closely related they were relative to conspecifics that did not share any recent genealogical history. Sherman (1981) noted that Belding's ground squirrels act nepotistically only for kin classes that remained alive for all generations – mothers, daughters, and sisters, and half-sisters – no other classes. If wood frog populations used in this study were the result of a single original and recent ancestry, it is possible that tadpoles would perceive each of the three cue treatments as 'kin'. Nevertheless, wood frog tadpoles clearly demonstrate kin-biased association preferences in similarly-composed wild populations (Cornell et al. 1989; Gamboa et al. 1991), and since wood frogs are highly philopatric (Berven and Grudzien 1990), spatially-separated populations of frogs may be fairly genetically distinct.

It is worth noting that the same prey in the same volume of water were used to produce all three cue types, and that the responses of receivers to disturbance cues and alarm cues were statistically similar. While the current study does not explicitly control for the chemical concentration of either cue, it does suggest that disturbance cues evoke an antipredator response similar to that seen in prey exposed to low concentrations of alarm cue. Other studies have found

lower responses of prey to disturbance cues relative to alarm cues (again, without controlling for cue concentrations) (Ferrari et al. 2008; Gonzalo et al. 2010). Interestingly, Gonzalo et al. (2010) noted similar responses to a conditioned predator odour the day after initial pairing with disturbance cues and alarm cues. However, after the first day, disturbance cue-paired odours were forgotten while alarm cue-paired odours were remembered up to nine days after initial conditioning. It is also worth noting that most studies examining disturbance and alarm cues extract them from separate individuals, while in my study, alarm cues were taken after individuals had released disturbance cues. Since disturbance cues are likely finite (Smith 1979) and involve nitrogenous waste products (Hazlett 1990a; Brown et al. 2012a), the alarm cues used in the current experiment may have not included any disturbance cues and thus evoked a less-than-normal fright response in tadpoles. However, this assertion assumes that disturbance cues are responsible for at least some portion of prey responses to chemical alarm cues, which is entirely speculative. Moreover, alarm cues used in this experiment were very dilute relative to other studies (0.05 tadpoles/ml vs. 0.025 to 0.17 tadpoles/ml in other studies; e.g., Ferrari et al. 2009a; Ferrari and Chivers 2009) and my tadpoles were relatively large compared to most studies of alarm cues in tadpoles. In either case, the current study generates many questions about how disturbance cues shape up relative to alarm cues in a natural predation context.

## Chapter 4: Background risk alters how tadpoles release and respond to disturbance cues<sup>1</sup>

### 4.1. Introduction

Previous experience with risk can dramatically influence the way prey perceive subsequent information about risk. Repeated exposure to stimuli indicating predation risk – such as through repeated exposure to alarm cues or the visual sight of a predator – are known to elicit a ‘high-risk phenotype’ (Brown et al. 2016; Crane and Ferrari 2016; Mitchell et al. 2016). These high-risk prey have altered stress reactivity, physiology, cognition, and behaviour relative to their low-risk counterparts (Brown et al. 2013; Ferrari et al. 2015b; Ferrari et al. 2015c; Ferrari et al. 2015d; Chivers et al. 2016; Mitchell et al. 2016). Yet, little is known regarding how prey rely on conspecific cues when they have previously experienced a high-predation risk environment. The ‘costly information hypothesis’ predicts that prey will rely more on social cues indicating risk when it is too risky to glean information about predators through personal observation (Boyd and Richerson 1985). Therefore, prey from high-risk environments are expected to rely more on conspecific cues than prey from low-risk environments (Webster and Laland 2008).

To explore how recent experience with risk affected both the production and response to disturbance cues, I tested the response of wood frog tadpoles (*Lithobates sylvaticus*) from high- and low-risk backgrounds (the receivers) to disturbance cues from high- and low-risk tadpoles (the donors). To establish the two risk regimes, larval tadpoles were conditioned to either low or high background risk through repeated exposures to either control water or injured

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<sup>1</sup> Most of the content of this chapter comes from the following publication. Changes have been made to avoid redundancy with other chapters and for consistency among chapters. KRBN conducted the experiment, analyzed the data, and wrote the first draft of the manuscript.

**Bairos-Novak KR, Mitchell MD, Crane AL, Chivers DP, & Ferrari MCO. (2017) Trust thy neighbour in times of trouble: background risk alters how tadpoles release and respond to disturbance cues. *Proc. R. Soc. B* 284:20171465.**

conspecific alarm cue, respectively (Ferrari et al. 2009b; Ferrari et al. 2015b). Tadpoles likely scale their responses according to the cumulative risk perceived in the environment, rely more on social information when personal experience about predation risk is costly to obtain (which it so often is), and meld multiple sources of information (e.g., disturbance cues  $\times$  alarm cues) when assessing risk. Therefore, I hypothesized that differences in a tadpole's background risk would affect their production and response to disturbance cues. I predicted that high-risk receivers could not afford to ignore disturbance cues relative to low-risk receivers (i.e., high-risk receivers would have a lower threshold of response). Finally, if high-risk individuals produce more disturbance cues than low-risk individuals when exposed to the same stimuli, receivers should respond more to high-risk disturbance cues relative to low-risk disturbance cues.

## **4.2. Methods**

### *4.2.1. Tadpoles and background risk*

Tadpoles were collected in early May of 2016 and raised similar to the previous experiments. The tadpoles in this experiment were all in Gosner stage 25 and all < 20 mm in total length, and so were not measured. I moved 30 different groups of 10 individuals to 3.7 l plastic pails filled with 1.5 l of filtered water for background risk exposures. Background risk exposures of either alarm cue or filtered water occurred 3 times daily for 5 days prior to testing, for a total of 15 exposures. Exposures took place between 1000 hours and 1700 hours CST at an inconsistent time throughout the day, with at least 1.5 h separating each exposure. I prepared alarm cues prior to each exposure by euthanizing 12 tadpoles via a blow to the head (using a mortar and pestle), emulsifying the bodies, mixing the result with 160 ml of filtered water, and filtering this solution through cotton gauze to remove any large pieces of tissue that remained (Ferrari et al. 2007; Ferrari and Chivers 2009; Ferrari and Chivers 2010). This preparation yielded enough alarm cue for eight injections (20 ml per injection containing  $\sim$ 1.5 tadpoles each). This alarm cue concentration was similar to previous studies and known to elicit a high-risk background phenotype in aquatic prey such as tadpoles (Gonzalo et al. 2010; Chivers et al. 2013; Lucon-Xiccato et al. 2016), and thus was used for tadpoles in the 'high-risk' treatment group. I used 20 ml of filtered water in the place of alarm cues for the relatively lower risk or 'low-risk' treatment group. Either low-risk or high-risk cues were consistently and similarly administered to the same pails containing tadpoles each day during the background risk exposure



period and each pail underwent a complete water change 1 h after the last conditioning event of the day to avoid habituation to the cues.

#### 4.2.2. Cue preparation and testing

To avoid the confounding effects of familiarity, I selected 8 high-risk donor tadpoles at random from 8 different high-risk pails to obtain high-risk cues, and similarly selected 8 low-risk donors from independent pails to produce low-risk cues. Undisturbed and disturbance cues were prepared according to similar methods described in section 2.2.2, with the exception that cues were created using 8 tadpoles in 320 ml of filtered water (0.025 tadpoles/ml). I selected a relatively lower concentration relative to my previous experiments using 0.05 tadpoles/ml in an attempt to increase the contrast between the antipredator responses of low- and high-risk tadpoles to disturbance cues. Tadpoles were tested within 2 h of cue preparation following the same protocols as in section 2.2.3.

#### 4.2.3. Statistical analysis

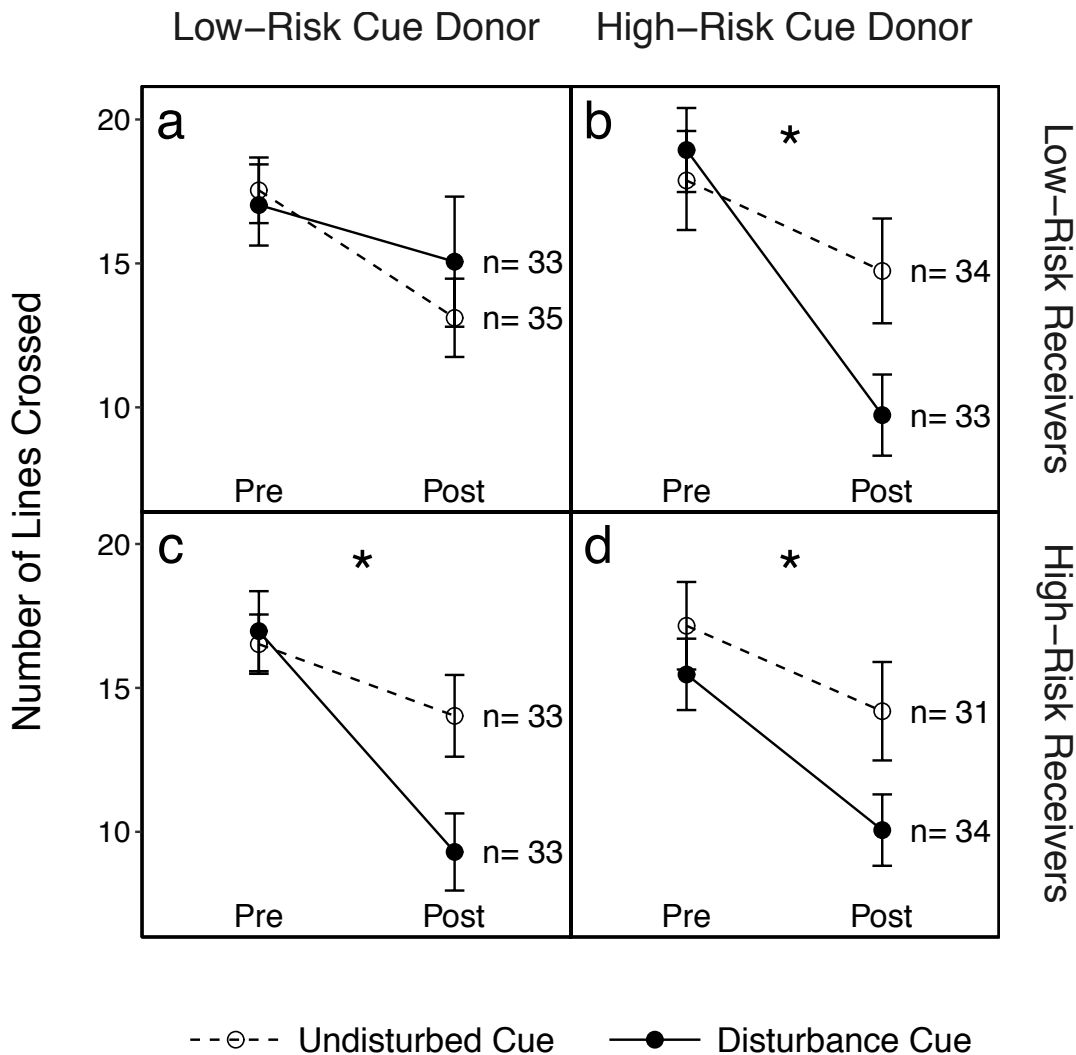
I tested for differences among tadpole pre-exposure line crosses using a 3-way ANOVA ( $Y_{pre\ lines} \sim X_{receiver\ risk} \times X_{donor\ risk} \times X_{cue\ type}$ ). I tested the relative change in tadpole line crosses using a 4-way repeated-measures analysis of variance (R-M ANOVA) testing the effect of cue donor risk (low vs. high), receiver risk (low vs. high), and cue type (undisturbed cue vs. disturbance cue) as between-subject factors, and time period (pre- vs. post-stimulus;  $W$ ) as the within-subjects factor ( $Y_{line\ crosses} \sim X_{receiver\ risk} \times X_{donor\ risk} \times X_{cue\ type} \times W$ ). I selected a different analysis for this experiment after inspecting the error terms of each model. The error term for a three-way ANOVA model was much larger than that of a 4-way R-M ANOVA, which treats the change in pre- and post-exposure line crosses similar to a random effect term in a mixed model. No outliers were removed from the dataset as all ANOVA assumptions were satisfied. All tests were two-tailed and I report  $P$ -values from Pillai's trace, as this conservative method reduces the likelihood of committing a Type I error. I used  $\alpha = 0.05$  to assess overall model significance and employed the Bonferroni correction ( $\alpha' = \alpha/k$ ) for multiple *post-hoc* tests when the analysis was rerun at lower factor levels in order to investigate significant interactions. Statistical analysis was conducted in R v.3.3.2 (R Development Core Team 2016) using the *afex* package (Singmann et al. 2016) and results were plotted using the *ggplot2* package (Wickham 2009).

### 4.3. Results

Pre-exposure line crosses did not differ across treatment groups. For the pre-exposure number of line crosses model ( $Y_{pre\ lines} \sim X_{receiver\ risk} \times X_{donor\ risk} \times X_{cue\ type}$ ), there were no significant fixed effects (2-way ANOVA, overall  $F_{7,258} = 0.54$ ,  $P = 0.80$ ,  $N = 266$ ), indicating equivalent pre-cue exposure line crosses among the different treatments. The mean  $\pm$  SE pre-exposure line crosses was  $17.2 \pm 0.5$  lines.

The decrease in line crosses from pre- to post-cue exposure changed depending on the cue type, donor risk, and receiver risk. I used a repeated-measures ANOVA model ( $Y_{line\ crosses} \sim X_{donor\ risk} \times X_{receiver\ risk} \times X_{cue\ type} \times W$ ) and found a significant 4-way interaction ( $F_{1,258} = 6.4$ ,  $P = 0.012$ ,  $N = 532$ ) indicating that the change in lines crossed depended on the risk level associated with the cue donor and the cue receiver as well as the type of cue used. This interaction stemmed from the fact that low-risk tadpoles did not alter their behaviour in response to low-risk disturbance cues (Fig. 4.1a; paired t-test,  $t_{32} = 0.93$ ,  $P = 0.36$ ,  $N = 33$ ,  $\alpha' = 0.01$ ), but showed a marked antipredator response when exposed to disturbance cues from high-risk conspecifics (Fig. 4.1b,  $t_{32} = 6.7$ ,  $P < 0.001$ ,  $N = 33$ ,  $\alpha' = 0.01$ ). The low-risk receiver response pattern differs from that of high-risk receivers who responded to disturbance cues from both low-risk tadpoles (Fig. 4.1c,  $t_{32} = 4.6$ ,  $P < 0.001$ ,  $N = 34$ ,  $\alpha' = 0.01$ ) and high-risk tadpoles (Fig. 4.1d,  $t_{33} = 4.5$ ,  $P < 0.001$ ,  $N = 34$ ,  $\alpha' = 0.01$ ).

When tadpoles responded to disturbance cues, they did so similarly across the different treatment combinations. High-risk receivers responded with a similar intensity to low- or high-risk disturbance cues (Fig. 4.1c/d, two-way R-M ANOVA interaction of receiver risk level  $\times$  pre/post-exposure:  $F_{1,65} = 1.2$ ,  $P = 0.27$ ,  $N = 134$ ,  $\alpha' = 0.025$ ). Similarly, the response of low- and high-risk receivers to high-risk disturbance cues was commensurate (Fig. 4.1b/d, two-way interaction of cue donor risk level  $\times$  pre/post-exposure:  $F_{1,65} = 4.3$ ,  $P = 0.043$ ,  $N = 134$ ,  $\alpha' = 0.025$ ).



**Fig. 4.1.** Mean ( $\pm$  SE) number of lines crossed by wood frog tadpoles from pre- to post-cue exposure in response to undisturbed conspecific cues (dashed lines and open circles) and disturbance cues (solid lines and closed circles) across low- (a+c) and high- (b+d) cue donor risk levels as well as low- (a+b) and high- (c+d) receiver risk levels. Asterisks represent significant responses to disturbance cues.

#### 4.4. Discussion

High-risk cue donors released disturbance cues that prompted more of a fright response in low-risk receivers compared to disturbance cues from low-risk donors. This means that high-risk donors may produce disturbance cues of increased quantity or quality, and/or different,

more potent chemical cues relative to low-risk donors. The latter is unlikely over the short-term, given that the time required to respond to a pursuing predator is often too rapid for major biochemical or physiological changes in nitrogen excretion of most anurans (Wright and Wright 1996; Wilkie 2002). However, high-risk individuals have increased foraging rates (Chuard et al. 2018) and altered diet and gut morphology (Relyea and Auld 2004), which may affect the biochemical composition of disturbance cues produced by each group. While the activity of tadpoles during the simulated disturbance chase was not explicitly recorded in this study, there were no apparent differences in the escape responses of low- and high-risk donors to the same physical disturbance used to obtain disturbance cues. Yet, individuals with the high-risk phenotype may have somewhat changed escape responses to predators (Ramasamy et al. 2017). High-risk donors may also produce more disturbance cues due to differences in their stress physiology relative to low-risk donors. For example, individuals from high-risk environments appear more reactive to some stressors and exhibit an increased physiological stress response (Boonstra et al. 1998; Brown and Bibost 2014; Ferrari et al. 2015b). Finally, my observed results may also be explained by the hypothesis that disturbance cues act as an antipredator signal to coordinate prey defenses. Other coordinated antipredator behaviours also increase with rising background risk levels. For example, three-spined stickleback populations with higher relative predation rates are known to inspect predators more than low-risk populations (Walling et al. 2004). In any case, the current study suggests that tadpoles can modify their disturbance cue output over a time period of five days or less and more work is required to elucidate the plasticity of disturbance cue production.

High-risk receivers responded more than low-risk receivers to the same disturbance cues produced by low-risk donors, likely due to a lowered minimum behavioural response threshold. Therefore, tadpole antipredator responses likely depend on knowledge of predation risk and the quantity of disturbance cue perceived, as affected by the number of cue donors and the concentration of disturbance cues in solution (Vavrek and Brown 2009; Brown et al. 2013). A lower response threshold has also been observed as a result of high background risk levels in some species of fish (Brown et al. 2001; Brown et al. 2006). While disturbance cues are relatively less reliable in terms of predicting risk compared to alarm cues (Ferrari et al. 2008; Ferrari et al. 2010), disturbance cues in high-risk environments are more likely to indicate credible predation risk.

Where tadpoles significantly responded to disturbance cues, I observed no difference in the magnitude of the antipredator responses to disturbance cues (Fig. 4.1b-d), indicating an all-or-nothing threshold response strategy to disturbance cues. Undisturbed cues decrease prey activity by 19% on average, while low-risk receivers responding to low-risk disturbance cues decreased activity by only 12%. All other combinations of disturbance cues decreased activity by 43% on average.

## **Chapter 5: General Discussion**

### **5.1. Summary of findings**

My main findings suggest that tadpoles are able to detect variation in the disturbance cues from others, do not differentiate between disturbance cues from close-relatives vs. less-related individuals, and that tadpoles from high predation risk environments release quantitatively or qualitatively different disturbance cues relative to low-risk tadpoles. In Chapter 2, tadpoles failed to respond to disturbance cues from familiar individuals, but responded to disturbance cues produced by strangers. This suggests that tadpoles habituated and ignored the ‘unreliable’ disturbance cues that were never followed by credible predation risk during the one-month familiarization period. In Chapter 3, tadpoles responded to disturbance and alarm cues from kin and putative non-kin similarly. This concurs with other studies of receiver responses to alarm cues from kin (Meuthen et al. 2014). Finally, in Chapter 4, high-predation risk tadpoles released and responded more to disturbance cues relative to low-predation risk tadpoles, suggesting that prey increasingly rely on disturbance cues in environments with more predation. Below, I take what is previously known regarding the function and evolution of disturbance cues and integrate it with the current thesis. I then conclude with some potentially fruitful avenues, given how little is known about disturbance cues.

### **5.2. Possible function(s) of disturbance cues in aquatic environments**

My results ultimately beg the question: what is the proximate function(s) of disturbance cues, and why did they ultimately evolve in the first place? Both remain a source of debate, as little is known about how disturbance cues mediate social information transmission (Chivers et al. 2012). Smith (1992) originally postulated 16 unique hypotheses regarding the evolution of alarm cues and many of these could apply to disturbance cues given their potentially voluntary production in response to predation, rather than as a by-product of predation events (Chivers et al. 2012; Wisenden 2014). The majority of these hypotheses assume that disturbance cues act as

a signal and are therefore produced in specific contexts. Again, I define signals as stimuli that are released by the sender to modify the behaviour of receivers in a way that benefits the sender (Otte 1974; Donath 2007).

One crucial part of this definition is the ability of prey to modulate their own production of stimuli in accordance with the context they find themselves in. While there is some evidence that disturbance cues may be associated with nitrogenous wastes and thus could be controlled via pre-existing excretion systems, no study to date has explicitly tested this idea. Male fish actively produce urine pulses in intrasexual competition to express their large body size and exert dominance over smaller same-sex subordinates while simultaneously advertising these same qualities to females (Almeida et al. 2005; Barata et al. 2007; Barata et al. 2008; Maruska and Fernald 2012; Bayani et al. 2017). Fish also release mating pheromones through their urine (Stacey et al. 1986; Scott and Vermeirssen 1994), and the volume of urine available greatly increases just prior to the mating season (Katsel et al. 1992 as cited in Sorensen and Stacey 1999). Thus, if disturbance cues do consist of urine pulses, prey may easily be in control of these processes. Given this, disturbance cues as signals could have presumably evolved through the process of cue ritualization. In Table 5.1, I propose 13 possible functions of disturbance cues as signals.

Of these 13 hypotheses regarding the function of disturbance cues, initiating group cypsis and shoal cohesion are the most supported. Tactile and chemical disturbance cues are known to increase shoal cohesion in fishes (Meuthen et al. 2016; Brown et al. unpublished data), and most disturbance cue studies demonstrate decreased activity in receivers (see Table 1.1). Indeed, chemical disturbance cues may coordinate group behaviours such as reduced activity and freezing, closer shoaling or schooling, and coordinated group dashing, all of which likely improve the survival odds for aquatic prey when faced with a predator (Smith 1992; Chivers et al. 1995; Crook and Davoren 2014).

Other hypotheses for disturbance cues remain untested but are supported indirectly in the literature. Disturbance cues may be used to initiate predator inspections in prey. Prey that engage in predator inspections of ambush predators are more likely to deter predators from attacking (Pitcher et al. 1986; Godin and Davis 1995; Walling et al. 2004), but also put themselves at risk if they are the only individuals inspecting the predator (Milinski 1987; Milinski et al. 1990). It is therefore unsurprising that groups composed of familiar or genetically-related individuals tend to

engage in a higher frequency of predator inspections (Chivers et al. 1995; Hesse et al. 2015), although this has never been observed in tadpoles. The frequency of predator inspections also increases within high predation risk environments (Walling et al. 2004), as does prey reliance on disturbance cues (see Chapter 4). Therefore, disturbance cues could, in theory, serve to increase or coordinate predator inspections among prey. Yet, Abreu et al. (2016) demonstrated that disturbance cues are mostly released in zebrafish that are chased by a predator (model) rather than prey exposed to a visual predator, and so the timing of disturbance cue production may preclude predator inspection events. In other words, prey likely do not rely on disturbance cues to coordinate predator inspections if disturbance cues are produced only after prey are chased by a predator, since predator inspections do little to deter predators after the attack sequence has begun. Another potential function of disturbance cues may be to cloak an individual's scent from aquatic predators, given the use of urea by the Gulf toadfish (*Opsanus beta*) to cloak its scent from nearby predators (Barimo and Walsh 2006). Since tadpole disturbance cues likely consist of pulses of ammonia, it remains to be seen whether ammonia pulses could also cloak the scent of tadpoles to nearby predators (Kiesecker et al. 1999; Manteifel et al. 2005). However, disturbance cues of fishes are most likely urea-based, and so this hypothesis could be explored further (Brown et al. 2012b)



**Table 5.1.** The proposed proximate functions of disturbance cues as signals, adapted from Smith (1992).

Receiver of Signal	Benefits (sender/receiver)	Function	Support	Comments regarding disturbance cues:
Predator	(+ / -)	<b>Startle effects:</b> startle, or surprise predators	×	No evidence to date.
Predator	(+ / -)	<b>Aposematism:</b> signal predator that prey is dangerous or unpalatable	×	Unlikely, given the widespread nature of disturbance cues in many prey that are entirely palatable.
Predator	(+ / -)	<b>Injure predator:</b> harm predators through release of toxic chemicals	×	No evidence to date.
Predator	(+ / -)	<b>Confusion, chemical camouflage, or sensory impairment:</b> misdirects, hides, or confuses predators such that they are not able to accurately detect or attacking prey	?	Untested to date. Urea pulses in gulf toadfish have been suggested to mask their scent from predators (Barimo and Walsh 2006).
Predator	(+ / -)	<b>Pursuit invitation/baiting:</b> lure predator into unsuccessful attacks, e.g., piping plovers (Ristau 1993)	?	Untested to date.
Predator	(+ / -)	<b>Pursuit inhibition/flagging:</b> signal predator that attacks will be unsuccessful, e.g., flagging deer	?	Untested to date.
2° predators	(+ / +)	<b>Predator attraction:</b> attract other predators that may disrupt the attack by the first predator	×	Unlikely, but may be the case for chemical alarm cues (see Chivers et al. 2012 for a review, Lönnstedt and McCormick 2015).
Predators of predator	(+ / +)	<b>Burglar alarm hypothesis:</b> attract predators of the initial predator that may disrupt the attack (Burkenroad 1943)	?	Untested to date.
Other prey	(+ / -)	<b>Behavioural manipulation:</b> manipulate other prey into fleeing and distracting the predator	×	Deceit as the sole function of disturbance cues is not sustainable (Trivers 1971), and prey may quickly learn to differentiate reliable cues from unreliable (Koops 2004).

Other prey (+ / +)	<b>Predator mobbing:</b> coordinate prey defensive attacks on predator	×	Very few observations exist to date of predator mobbing in aquatic prey (but see Lachat and Haag-Wackernagel 2016).
Other prey (+ / +)*	<b>Initiate predator inspection:</b> simultaneous e.g., silence or hiding, reducing change of predator detecting the group	?	Untested to date. While predator inspections increase in familiar and/or genetically-related fish shoals, since disturbance cues are released while prey are being chased, they may have little effect on the predation outcome.
Other prey (+ / +)*	<b>Initiate group crypsis:</b> simultaneous e.g., silence or hiding, reducing change of predator detecting the group	✓	Most prey exhibit reduced activity in response to disturbance cues, in addition to in the current study.
Other prey (+ / +)*	<b>Increase shoal cohesion:</b> initiate tighter grouping, decreasing the distance between prey and thus improving survival of the group	✓	Survival increased when prey exposed <i>a priori</i> to disturbance cues and some evidence of shoal cohesion in cichlids (Brown et al. unpublished data, Bairos-Novak et al. unpublished data).

\*May also function as a reliable cue (0, +) rather than as an honest signal (+ / +), if disturbance cues are not under the control of the donor individual.

### 5.3. Ultimate evolution and maintenance of disturbance cues

Since disturbance cues could also act as a cue for predators to better locate and target prey in the aquatic system, it is likely that they are produced because they elicit some positive inclusive fitness benefits for the releaser (Maynard Smith 1965). Ultimately, disturbance cues could have arisen as a signal through cue ritualization, as previously discussed. In Table 5.2, I describe 7 hypotheses concerning the potential fitness benefits of disturbance cues as signals. Of these, only two hypotheses show mixed support in the literature and in the current thesis.

Disturbance cues could be maintained as signals if they benefitted the group and/or the sender over the long run (Chivers et al. 2012; Wisenden 2014). For example, if they function as a way of coordinating prey antipredator defenses in order to increase overall survival of the group (+ / +), this would be an example of byproduct mutualism. Alternatively, even if disturbance cues decrease the fitness of the sender (-, +), they could be maintained in populations through reciprocal altruism, as is likely the case for alarm calls in alarm-calling sciurids (Maynard Smith 1965; Hare and Murie 1996; Hare and Warkentin 2012). Both reciprocal altruism and byproduct mutualism hypotheses concur with the fact that disturbance cues increase group cohesiveness and shoaling in aquatic prey (see Table 5.1). Reciprocal altruism may also involve increased reliability assessment by the receivers in order for prey to determine if group members have produced cues reliably with predation risk stimuli in the past. As discussed at the end of Chapter 2, tadpoles ignored unreliable cues from familiar individuals, arguably because they were never seen as 'reliable'.

Kin selection is another viable hypothesis regarding the long-term maintenance of disturbance cues as a signal (Chivers et al. 2012; Wisenden 2014). Here, individuals are expected to increase their inclusive fitness by emitting more, or more potent, disturbance cues when their cumulative coefficient of relatedness to group members is higher. However, since most adult aquatic prey tend to shoal with unrelated individuals (Krause et al. 2000), disturbance cues are less likely to be maintained via kin selection. However, this could still be the case for wood frog tadpoles, despite the negative findings of Chapter 3 regarding kin-biased responses of receivers. Since any disturbance cue represents a credible risk in the environment, it may always be advantageous to respond to disturbance cues from both close kin and non-kin (Meuthen et al. 2014).

Whatever disturbance cues may be, how they function, and their ultimate evolution remains a mystery to biologists. Additionally, certain species are liable to employ disturbance cues in different ways, for example, shoaling forage fishes may be more reliant on disturbance cues as signals to alert conspecifics, whereas disturbance cues in tadpoles may simply act as a cue that is released in order to deter predators from a successful attack. A species' life history is likely to impact what the potential inclusive fitness benefits of disturbance cues may be. For example, species that shoal extensively with kin for most of the year rather than non-kin are more likely to maintain disturbance cues as signals through kin selection, rather than reciprocal altruism. In these species, one would predict that conspecifics producing disturbance cues may do so dependent on their perceived audience, such as when they are shoaling with kin compared to a non-kin shoal.

**Table 5.2.** The possible ultimate causes leading to the evolution of disturbance cues as signals, adapted from Smith (1992).

<b>Evolution via</b>	<b>Support</b>	<b>Comments regarding disturbance cues:</b>
<b>Individual selection:</b> save oneself from predation	×	Most proposed functions of disturbance cues when received by the individual or by the predator are not well supported or investigated, with the exception of urea cloaking by the gulf toadfish (Barimo and Walsh 2006).
<b>Reduce overall predation:</b> reduce future attacks through reduced predator success in local area and/or on fellow conspecifics	×	Unlikely, since prey likely benefit from reduced competition for resources with some predation.
<b>Future mating success:</b> save mates, avoid cost of mate replacement or brood loss	×	Unlikely for current study, given tadpoles are not reproductively differentiated.
<b>Sexual selection for altruistic behaviour:</b> appear attractive to females for 'altruism' towards conspecifics (analogous to concept of social prestige in humans)	×	Unlikely for current study, given tadpoles are not reproductively mature at the time of disturbance cue production.
<b>Kin selection:</b> increase survival of offspring or other genetically-related individuals	×/?	No difference in receiver responses (Chapter 3). Kin recognition and preference for association in some species (e.g., tadpoles), but many species of fishes do not prefer to shoal with kin (see Krause et al. 2000).
<b>Byproduct mutualism:</b> alert others because it increases one's own individual fitness	√/?	Some supporting evidence, given disturbance cues may initiate collective antipredator defenses such as tighter shoal cohesion.
<b>Reciprocal altruism:</b> alert others while decreasing individual fitness, as the behaviour will be reciprocated back. Employ 'tit for tat' strategies when engaging with repeatedly-encountered individuals and recall past individual reliability	√/?	Some supporting evidence, given disturbance cues may initiate collective antipredator defenses such as tighter shoal cohesion. This method would involve more reliability assessment by the receivers (as may have been observed in Chapter 2).

#### **5.4. Summary, Importance, and Future Directions**

The results of the current thesis are inconclusive as to whether disturbance cues act as a signal in aquatic prey such as tadpoles. They reveal that prey can detect variation in disturbance cues (Chapters 2 and 4) and prey altered their disturbance cues after they had experienced a high-risk environment (Chapter 4), yet, more work is needed to determine if disturbance cues are released as per the definition of a signal. With this in mind, if prey are able to modulate disturbance cues based on their audience or group members, this may be evidence of disturbance cues as alarm signals. Specifically, if grouped aquatic prey respond more to the same disturbance with more, or more potent, disturbance cues, this may be evidence of disturbance cues acting as a signal for the individuals releasing disturbance cues. Additionally, other factors that may be of importance are the size of the group and the familiarity/kinship of the group that releases the disturbance cues. The current study was limited to only examining the effects of familiarity/kinship on the receivers of disturbance cues. Future experiments should examine prey responses to disturbance cues obtained from isolated individuals, unfamiliar, or familiar groups to determine if prey modulate disturbance cues in response to different audiences. Additionally, group size is likely to affect the antipredator responses of prey to disturbance cues, with familiarity and reliability effects declining with increasing group size (as well as the cognitive demands for remembering reliable conspecifics).

The chemical composition of disturbance cues and their extent and overlap among aquatic prey is a source of contention. A key component of disturbance cues appears to include a pulse of urea or ammonia, for fish and tadpoles, respectively (Munro 1957; Hazlett 1985; Kiesecker et al. 1999; Manteifel et al. 2005; Vavrek et al. 2008; Brown et al. 2012b). However, molecular analyses and chemical assays of disturbance cues are still required to confirm this. Also, while tadpoles and fish are known to respond to disturbance cues, the function and ultimate evolution of disturbance cues is likely independent and different among different taxa. Wood frog tadpoles do not form persistent shoals as do fishes, for example, and thus, other aquatic species such as shoaling forage fishes may be more likely to rely on disturbance cues as conspecific

antipredator signals. More work with disturbance cues needs to be done in aquatic species that live in highly social groups or who maintain consistent territories with their neighbours, such as schooling prey and coral reef fishes. These species are more likely to consider past reliability when tuning their antipredator responses to conspecific disturbance cues.

Most studies have failed to properly disentangle familiarity effects from kinship effects, and laboratory studies tend to produce different results relative to those of field studies (Krause et al. 2000; Griffiths 2003). Studies attempting to control for both have often shown that familiarity overrides genetic relatedness (e.g., Hare and Murie 1996; Liebgold and Cabe 2008), yet, the comparison is further complicated by the extent of familiarity and genetic-relatedness. Both are continuous variables (e.g., how long is the familiarization period? What is the average coefficient of relatedness among group members?), and both may interact with one another synergistically. Thus, there is a need for common garden experiments that manipulate both familiarity and kinship in order to map out the 3D response plane of these two variables. Much like the nature vs. nurture debate, the answer for kinship vs. familiarity is likely in the milieu, with positive benefits dependent on both variables.

Disturbance cues may represent an entirely novel animal signalling system that could impact how we manage all aquatic species, and may yield practical applications in terms of aquatic prey management and conservation. Specifically, disturbance cues may contribute to the observed Allee effects in wild populations of aquatic prey. Allee effects are density-dependent population growth rates, such that at low population sizes the probability of extinction is higher than ordinary populations (Allee 1931; Courchamp et al. 1999; Stephens et al. 1999). Allee effects often manifest in prey populations that use cooperative group defenses or collective vigilance to avoid predators (Courchamp et al. 1999; Brashares et al. 2010) For example, it has been suggested that a decrease in collective vigilance and alarm calling towards predators as a result of small population sizes has only exacerbated the decline of the critically-threatened Vancouver Island marmot, *Marmota vancouverensis* (Brashares et al. 2010). If disturbance cues serve as a signal to initiate cooperative antipredator behaviour, as speculated in this thesis, the communication of risk among prey may breakdown at low population sizes, resulting in

increased predation and leading to inverse density-dependent effects. Additionally, human pollution and recreational activities such as boating and ecotourism could serve to both confound or increase the frequency of disturbance cues produced by aquatic organisms, thus making disturbance cues undetectable or unreliable, respectively. It remains unknown how much prey rely on disturbance cues relative to other cues indicating risk in wild populations. Alarm cues and predator odours may still represent credible risk in the environment, and so prey would presumably increase their reliance on these cues when communication via disturbance cues deteriorates at low population levels. Understanding the antipredator behaviour of amphibians in general is of increasing importance for conservation biologists, as amphibians have faced increasingly high mortality in the wild due to invasive species that outcompete or consume amphibians, increased disease, and low breeding success in captivity (Dodd Jr. and Seigel 1991; Kats and Ferrer 2003; Murphy and Gratwicke 2017). The study of sensory ecology of disturbance cues is ripe for the picking, and may drastically change the way ecologists – and the public – think about communication in aquatic species.

### **Ethics Statement**

All experimental manipulations were approved by the University of Saskatchewan Animal Care Committee under protocols 20140014 and 20160006, in accordance with the Canadian Council on Animal Care.



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