



The development of alarm call behaviour in mammals and birds

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Alarm calling is a widespread antipredator behaviour. Although the function and evolution of alarm call behaviour have long been studied in detail, only in the last decade has there been an upsurge in research into its development. Here, we review the literature on the development of alarm call production (the delivery of calls with a specific set of acoustic features), alarm call usage (the use of calls in particular contexts) and alarm call responses (the responses to calls produced by others). We detail the mechanistic processes that may underlie the development of each aspect, consider the selection pressures most likely to explain the relative importance of these processes, and discuss the substantial variation in developmental rates found both between and within species. Throughout, we interpret existing findings about age-related differences in alarm call behaviour from two major communicatory viewpoints: the idea that signals carry information from sender to receiver, with young taking time to acquire adult-like skills; and the possibility that signals are used to manage the behaviour of receivers, with young behaving adaptively for their age. We conclude that a broader use of various techniques (e.g. cross-fostering and temporary removals), the formation of stronger collaborative links with other disciplines (e.g. physiology and neurobiology) and the initiation of new research avenues (e.g. kleptoparasitism) will ensure that studies on the development of alarm call behaviour continue to enhance our understanding of such topics as the evolution of communication and language, kin selection and cognitive processing.

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Alarm calling, the giving of particular vocalizations in the face of impending danger, is a key antipredator strategy that has evolved in a wide range of species (Caro 2005). Alarm call behaviour, as with all vocal communication, comprises three aspects: the delivery of calls with a specific set of acoustic features (call production); the use of calls in particular contexts (call usage); and the response to calls produced by others (call responses). Although there is often an obvious selfish selection pressure on receivers to respond to alarm calls (they may be more likely to survive if they do), their production can appear altruistic: in giving a signal that enhances the likelihood of others escaping, callers may attract the attention of the predator themselves. Studies of alarm call behaviour have therefore proved invaluable for our understanding of such issues as kin selection, nepotism, reciprocal altruism and cooperation (Sherman 1977; Hoogland 1996; Krams et al. 2006; Wheeler 2008). Similarly, research into alarm calling has provided many insights into the cognitive processes underlying signal perception (Blumstein 1999) and the evolution of communication (Spinozzi 1996; Evans & Evans 2007), including human language (Kuhl 1994; Werker & Yeung 2005). Clearly, therefore, alarm call behaviour is of

interest and relevance to researchers in many fields, and so it is not surprising that such a large literature exists on the subject (reviewed in Caro 2005).

Until recently, that literature had contained relatively few studies focusing on the development of alarm call behaviour. One likely explanation for the paucity of such research is the difficulty of acquiring the relevant data: alarm calling by young often occurs relatively rarely and unpredictably, and a long time is needed to determine fully the developmental trajectories present within a species. However, the establishment of many more long-term field studies and innovation from scientists, particularly in the last decade, has led to a rapid rise in research into the development of alarm call behaviour in both mammals and birds (Table 1). This increase in research interest is welcome, because developmental studies can inform us about the importance of various selection pressures, such as local environmental conditions (Lima & Dill 1990; Berger et al. 2001), can help elucidate the relative importance of kin selection, reciprocal altruism and direct benefits (Sherman 1977), and can provide valuable insights into functional signalling and thus the evolution of communication (Kuhl 1994; Blumstein 1999). Studies investigating the development of alarm call behaviour also provide an excellent opportunity to compare two conflicting viewpoints that have arisen with respect to animal communication: that signals are used to transfer information

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Table 1
Studies examining the development of alarm call behaviour in mammals and birds

Species	Aspect*	Method†	Source	Summary
<i>Mammals</i>				
Belding's ground squirrel, <i>Spermophilus beldingi</i>	U	O & E (LP)	Robinson 1981	Juveniles do not discriminate between predators and nonpredators
	R	E (PB)	Mateo 1996a, b	Young can discriminate between calls (measured by heart rate) before emergence, but responses become adultlike before dispersal at 7 weeks
	R	E (PB)	Mateo & Holmes 1997, 1999a, b	Early rearing environment and exposure to dams affect the rate of response development
California ground squirrel, <i>Spermophilus beecheyi</i>	R	E (LP, MP)	Hanson & Coss 1997	Juveniles show more urgent responses to chatters (terrestrial threat) and less urgent responses to whistles (avian threat) compared to adults
	R	E (PB)	Hanson & Coss 2001b	Compared with adults that treat a hawk as a more immediate threat than a dog, juveniles treat both with equivalent urgency
Richardson's ground squirrel, <i>Spermophilus richardsonii</i>	R	E (MP, PB)	Wilson & Hare 2006	Like adults, juveniles respond to ultrasonic alarm signals by increasing their vigilance
Thirteen-lined ground squirrel, <i>Spermophilus tridecemlineatus</i>	R	E (PB)	Schwagmeyer & Brown 1981	Juveniles are more likely not to respond to certain alarm calls than adults
Yellow-bellied marmot, <i>Marmota flaviventris</i>	P	O	Blumstein & Munos 2005	Alarm calls of young are higher pitched than those of adults
Great gerbil, <i>Rhombomys opimus</i>	P	E (MP, PB)	Randall et al. 2005	Calls of pups and subadults are higher pitched than those of adults
Pika, <i>Ochotona princeps</i>	U	O	Ivins & Smith 1983	Young give calls at similar rate and duration in both predator and nonpredator contexts
Goeldi's monkey, <i>Callimico goeldi</i>	R	E (PB)	Masataka 1983a	The responses of young (alarm calling and/or freezing) bear no resemblance to adult responses
Squirrel monkey, <i>Saimiri sciureus</i>	R	E (MP, PB)	Herzog & Hopf 1984	Responses of socially isolated young resemble responses of mother-reared infants
	R	E (PB)	McCowan et al. 2001	Infants gradually develop an adult-like response to alarms over the first year of life
Vervet monkey, <i>Chlorocebus aethiops</i>	P, U, R	O & E (PB)	Seyfarth & Cheney 1980, 1986	Much of the adult repertoire is recognizable in calls of young infants
	R	O & E (PB)	Hauser 1988	Young are predisposed to use calls correctly but need refinement
Japanese macaque, <i>Macaca fuscata</i>	R	O & E (PB)	Masataka 1983b	Responses develop entirely as the result of experience
	R	O & E (PB)	Masataka 1983b	Responses are affected by the exposure rates of superb starling alarm calls
Bonnet macaque, <i>Macaca radiata</i>	R	E (PB)	Ramakrishnan & Coss 2000	1-year-old infants rarely respond to alarm calls, 2-year-olds respond to any stimulus, whereas responses of 3-year-olds are similar to those of adults
Barbary macaque, <i>Macaca sylvanus</i>	R	O & E (PB)	Fischer et al. 1995	No marked difference between adults and juveniles when responding to adult alarms, but juveniles more likely to flee to juvenile alarms
	R	E (PB)	Fischer et al. 2000	Juveniles generally show stronger responses than adults
Chacma baboon, <i>Papio cynocephalus ursinus</i>	R	E (PB)	Fischer et al. 2000	At 2.5 months infants fail to respond whereas at 4 months they respond irrespective of call type. At 6 months they show adult-like responses
Verreaux's sifaka, <i>Propithecus verreauxi verreauxi</i>	R	E (PB)	Fichtel 2008	Young infants flee towards adults and only show adult-like responses at 6 months (physical independence)
Meerkat, <i>Suricata suricatta</i>	P	O	Hollén & Manser 2007a	Calls of young are higher pitched and of longer duration than those of adults
	U	O	Hollén et al. 2008	Young alarm call more in response to nonthreatening species compared to adults
	R	O & E (PB)	Hollén & Manser 2006	Newly emerged young flee down burrows irrespective of call type and approach adult-like responses over the following 6 months
<i>Birds</i>				
Mallard, <i>Anas platyrhynchos</i>	R	E (PB)	Miller & Blaich 1986	Birds older than 48 h show lower levels of freezing than younger birds in response to maternal alarm calls
	R	E (PB)	Miller et al. 1990	Socially reared devocalized ducklings show greater levels of freezing than socially isolated devocalized ducklings
Laughing gull, <i>Larus atricilla</i>	R	O & E (PB)	Impeken 1976	Responsiveness to alarm calls is affected by prenatal exposure to these calls
Common cuckoo, <i>Cuculus canorus</i>	R	E (PB)	Davies et al. 2006	Cuckoo chicks show innate pretuning to their host species' alarms, but need exposure to calls for the silent gaping response to develop
Dunnock, <i>Prunella modularis</i>	R	E (PB)	Davies et al. 2004	Cross-fostered nestlings still respond specifically to their own species' alarms but less strongly than normally raised nestlings
Robin, <i>Erithacus rubecula</i>	R	E (PB)	Davies et al. 2004	Cross-fostered nestlings still respond specifically to their own species' alarms but less strong than that of normally raised nestlings
Reed warbler, <i>Acrocephalus scirpaceus</i>	R	E (PB)	Davies et al. 2004	Cross-fostered nestlings still respond specifically to their own species' alarms but less strong than that of normally raised nestlings
Pied flycatcher, <i>Ficedula hypoleuca</i>	R	E (PB)	Korneeva et al. 2006	Defensive behaviour develops as the auditory sensitivity to certain frequencies matures
White-browed scrubwren, <i>Sericornis frontalis</i>	R	E (PB)	Maurer et al. 2003	Nestlings acquire the ability to respond appropriately to alarm calls late in the nestling period
	R	E (PB)	Platzen & Magrath 2005	Nestlings react more strongly to calls posing greater danger, appropriate to their stage of development
	R	E (PB)	Magrath et al. 2006	Young respond appropriately to aerial alarm calls coinciding with becoming vulnerable to aerial attack
Willow tits, <i>Parus montanus</i>	R	E (PB)	Rajala et al. 2003	Juveniles are more likely than adults to flee after hearing conspecific alarm calls

Table 1 (continued)

Species	Aspect*	Method†	Source	Summary
Great tits, <i>Parus major</i>	R	E(PB)	Rydén 1978a, b	Young only develop a response to aerial alarm calls late in the nestling period
	R	E (PB)	Rydén 1980	Nestlings raised in an environment dominated by high-pitched sounds subsequently show a decreased responsiveness to aerial alarm calls (high pitched)
	R	E (MP)	Kullberg & Lind 2002	Naïve fledglings do not respond differently to a model of a predator than to a model of a nonpredator
Red-winged blackbird, <i>Agelaius phoeniceus</i>	R	E (PB)	Madden et al. 2005	Chicks do not develop a response to their foster species' alarms
Brown-headed cowbird, <i>Molothrus ater</i>	R	E (PB)	Madden et al. 2005	Chicks do not develop a response to their foster species' alarms

* The aspect of alarm call behaviour that was investigated: P = production; U = usage; R = responses.

† The method used to investigate the development of alarm call behaviour: O = observations (including natural sound recordings of alarm calls); E = Experiments (LP = live predator presentation; MP = model predator presentation; PB = playbacks; where playbacks were used, natural sound recordings or predator presentations used to collect alarm calls for the experiments are not included).

between senders and receivers, and that they are used to manage the behaviour of receivers.

Ever since the seminal work demonstrating that vervet monkeys, *Chlorocebus aethiops*, produce acoustically distinct alarm calls to various predators, and that receivers respond in different, adaptive ways to them (Seyfarth & Cheney 1980, 1986), numerous studies have concluded that alarm calls include information about the urgency of the threat and/or the type of predator (Macedonia & Evans 1993; Manser 2001; Leavesley & Magrath 2005). Consequently, alarm calling has often been deemed referential, that is, conveying encoded information to receivers about objects and events in the external environment (Evans 1997), and this linguistically inspired, meaning-based view of vocal communication has become the predominant way of thinking. However, some researchers argue that the 'information transfer' perspective is problematic: it implies a cooperative venture between sender and receiver, which need not be the case; and, by proposing that the acoustic structure of calls bears no relation to their function, it adds an unnecessary level of complexity to the process (Owings & Morton 1998; Owren & Rendall 2001). A more fundamental standpoint focuses on call structure rather than call meaning. According to this 'assessment-management' view, callers use vocalizations to elicit affective responses in others, thereby altering the behaviour of these individuals to the caller's advantage, but not necessarily that of the receiver (Owings & Morton 1998). Receiver responses can be unconditioned, being produced directly by the energy in the signal itself, or conditioned, resulting from past interactions where the signal was coupled with a certain reaction (Owren & Rendall 2001).

From the information transfer perspective, young individuals have to develop the ability to encode correct information in the acoustic structure of alarm calls, to provide the correct information through their use of calls, and to decode information provided by the alarm calls of others. From the assessment-management perspective, the behaviour of young individuals must be understood in terms of their current needs: young will produce, use and respond to alarm calls in a way that is functional and adaptive for their particular developmental stage and that helps them cope with age-dependent risks. We believe that both approaches have merit, and that they are not necessarily mutually exclusive: young animals have both to survive their current environment and, simultaneously, anticipate future conditions. Here, we therefore interpret existing findings on the development of alarm call behaviour in light of both viewpoints. We consider alarm call production, usage and responses in turn, although it is worth noting that far more is currently known about the latter (Table 1). For each aspect we review the existing literature, considering the relative importance of, and evidence for, the different mechanistic

processes (genetic predispositions, physical and neurological maturation, physiological changes and learning) that may separately or in combination underlie the development of behaviour, and suggest under what ecological and social situations each might be most likely to play a role. We also discuss the substantial variation in developmental rates found both between and within species. Throughout the review we provide suggestions about the broader use of established techniques, potentially fruitful collaborations with other disciplines and ideas for future research directions, with particular emphasis on how these might help to tease apart, or reconcile, ideas about information transfer and assessment-management.

DEVELOPMENT OF ALARM CALL PRODUCTION

Early research concluded that alarm calls are fully formed in structure at first appearance in the vocal repertoire. For example, Seyfarth & Cheney (1980, 1986) described the alarm calls first given by infant vervet monkeys as acoustically indistinguishable from adult calls. However, the great majority of studies reporting no modification of alarm calls during development were conducted more than two decades ago when sophisticated analytical tools were not available (reviewed in Seyfarth & Cheney 1997). Rather than visually examining spectrograms to quantify the similarity of sounds, researchers nowadays process acoustic signals using automated digital techniques (e.g. Baker & Logue 2003). Probably as a result, recent studies have shown that alarm calls do show some plasticity. In yellow-bellied marmots *Marmota flaviventris* (Blumstein & Munos 2005), great gerbils, *Rhombomys opimus* (Randall et al. 2005) and meerkats, *Suricata suricatta* (Hollén & Manser 2007a), for example, the alarm calls of young are higher pitched than those of adults. The alarm calls of young meerkats are also longer in duration, more modulated, noisier and have their main energy at higher frequencies than those of adults (Hollén & Manser 2007a). Hence, although young produce alarm calls that resemble the general structure of adult calls, there are often discernible differences.

One possible reason for these age-related differences is that there has been strong selection pressure for juvenile alarm calls to be inherently more alerting or 'plosive' than those of adults, because of the higher vulnerability of young individuals to predation (Holmes 1984). Particular sounds stimulate brainstem circuitry directly and induce changes in the attention, arousal, motivation or emotion of the receiver (Eaton 1984; Owren & Rendall 2001), so by producing alarm calls of a certain structure young might manage the behaviour of nearby adults in a way that reduces the risk to the young themselves. This might explain why, for example, the alarm calls of juvenile yellow-bellied marmots cause adults to suppress

their foraging and increase their vigilance to a greater extent than the alarm calls of other adults (Blumstein & Daniel 2004). Receivers need not necessarily benefit from a manipulation of their behaviour (Owren & Rendall 2001), but because calls from juvenile marmots are likely to be produced by offspring or other young relatives in a matriline, enhancing the detection of predators and thus increasing the survival likelihood of the caller would, in this case, also provide kin-selected benefits to the adults involved (Blumstein & Daniel 2004).

To investigate the potentially plosive nature of alarm calls requires detailed acoustic analyses, focusing on features such as sharp onsets and dramatic frequency and amplitude modulations that are known to elicit affective responses in receivers (Owren & Rendall 2001). If the inherent structure of an alarm call is important, we would predict that such characteristics are more apparent in those calls that result in a stronger response. To confirm the relative salience of different acoustic parameters, computer-synthesized calls could be played back to the target animals. Playbacks of such manipulated calls have yet to be used in the investigation of alarm call development, but have been successfully used in other contexts (Masataka 1983a; Reby et al. 2005). In Goeldi's monkeys, *Callimico goeldi*, for example, researchers altered particular frequency and temporal features of adult alarm calls and played them back to other adult group members (Masataka 1983a). Receiver responses changed distinctly with an increase of only 0.2 kHz in the frequency range, whereas there was no discernible effect of variants of duration, centre frequency and bandwidth (the kind of features that do not necessarily have an impact on nervous systems). This method could therefore be useful in determining not only the importance of particular acoustic parameters, but also the scale of acoustic differences needed to evoke different receiver responses.

Age-related differences in alarm call production need not necessarily be adaptive, but might instead be the consequence of developmental constraints. The most obvious possible constraint on juvenile call production is physical maturation. For example, fundamental and peak frequency-related parameters, which determine call pitch, are likely to change as the length of the vocal tract and the size of the resonance cavities increase during growth (Fitch & Hauser 1995). Vocal control also improves as individuals grow older (Boliek et al. 1996; Scheiner et al. 2002), possibly explaining why noisy call types which require relatively little control over the vocal apparatus (Lieberman 1986) are often those that are produced during the first days of life (e.g. Hollén et al. 2008). Although the research focus to date has been on motor constraints, neurological development in the relevant brain areas might prove equally crucial. Unfortunately, whereas the neural basis of birdsong has long been established and much has been discovered about how different brain nuclei and their connecting pathways contribute to song learning (reviewed in Bottjer & Arnold 1997; Brainard & Doupe 2002; Nottebohm 2005), very little is known about the neural mechanisms underlying alarm calling. We do know that certain brain structures play a key role in the development of antipredator defence behaviour (Wiedenmayer 2009), but there is an urgent need for insight into how alarm calls are encoded neurologically and how neural changes relate to age-specific changes in alarm call production.

Acoustic differences in the alarm calls produced by different age groups might also arise if physiological arousal levels differ (see Hanson & Coss 2001a). Changes in arousal have been shown to influence parameters such as pitch and duration in nonalarm calls (Scheiner et al. 2002; Rendall 2003), and juveniles may be more aroused because they are generally more vulnerable (Holmes 1984). Valuable light could be shed on this possibility by measuring some indicator of arousal, such as heart rate, at the time of an alarm

call (see Rydén 1980; Evans & Gaioni 1990; Mateo 1996a). Assessment of glucocorticoid concentrations in faeces (e.g. Blumstein et al. 2006) could also help to establish whether different age groups display baseline differences in arousal and whether this affects their production of alarm calls. In some species, elevated corticoids can also facilitate learning and memory (Hanson & Coss 2001a; McGaugh 2004), so future work should explore whether an increase in arousal could function to promote acquisition of alarm call behaviour rather than being the direct cause itself (see Mateo 2006).

Inherent differences in the anatomy, neurology or physiology of individuals of different ages might result in juvenile calls that are less plosive or, if the transfer of information is important, that denote something less threatening than those produced by adults. This would help to explain such findings as the reduced flight response and slower reaction times of adult vervet monkeys, bonnet macaques, *Macaca radiata*, and California ground squirrels, *Spermophilus beecheyi*, to juvenile alarm calls compared to those of other adults (Seyfarth & Cheney 1980; Ramakrishnan & Coss 2000; Hanson & Coss 2001b); given the greater vulnerability of young, it seems unlikely that there will have been adaptive selection on juvenile calling to be less evocative than that of adults. In other species, developmental constraints might result in juvenile alarm calls that are less informative than those of adults. For example, if adult yellow-bellied marmot calls really do signal threat urgency (Blumstein & Armitage 1997), perhaps juvenile calls only suggest the general presence of predators. The increased vigilance by adult receivers in response to juvenile alarm calling (Blumstein & Daniel 2004) might therefore be because there is a greater need for private assessment of the current risk compared to when another adult has called.

A further consequence of differences in the structure of calls produced by adults and juveniles is that receivers might be able to identify callers of different age classes (Blumstein & Daniel 2004). Any difference in response might therefore arise, not because of induced reactions to particular acoustic characteristics or because of differences in the information content of the call itself, but because the receiver has chosen to respond differently depending on the identity of the caller. For example, because juveniles are potentially less reliable at providing accurate information, for example they might detect predators less frequently or make more mistakes in their use of alarm calls (see Development of alarm call usage), receivers might choose to respond less strongly to them (e.g. Hanson & Coss 2001b) or, alternatively, they might increase their vigilance more in response to juvenile alarm calling (e.g. Blumstein & Daniel 2004) to obtain a suitably accurate assessment of the current predation risk.

There is some evidence that adult receivers are capable of discriminating between reliable and unreliable callers in general (Hare & Atkins 2001; Blumstein et al. 2004), but no studies have yet examined whether relative reliability is actually an important reason why receivers respond differently to adult and juvenile alarm callers. To do so, calls and contexts could be artificially manipulated: the perceived reliability of different individuals could be altered by pairing their alarm calls with or without model predators, with subsequent assessment of receiver responses (see Hare & Atkins 2001; Blumstein et al. 2004). Moreover, because juveniles do not necessarily appear capable of distinguishing between reliable and unreliable callers (Robinson 1981; Ramakrishnan & Coss 2000), similar experiments could be used to determine when such discrimination ability develops. By combining manipulations of perceived reliability with the playback of synthesized calls (see above) it would be possible to begin teasing apart the relative importance of inherent call characteristics and any potential information contained within them, as well as

establishing why juvenile alarm calls are more evocative than adult calls in some species, but less so in others.

DEVELOPMENT OF ALARM CALL USAGE

A prerequisite for effective alarm call usage is the recognition of predators (reviewed in Caro 2005). There is compelling evidence that some species are capable of recognizing predators when they are first encountered (Curio 1993; Veen et al. 2000; Göth 2001). Such recognition might be innate, but this may often be hard to demonstrate because other processes could play a role before the behaviour is first expressed and can thus be measured. For example, amphibians can learn to recognize future predators while in the egg (Ferrari & Chivers 2009), human babies can learn to distinguish sounds while in utero (Chamberlain 1998), and the young of species that spend the first few weeks of life underground may have had some exposure to the sounds of predators and conspecifics prior to emergence (Mateo 1996a). A fixed unlearned recognition ability on first exposure to predators has the advantage that individuals stand a better chance of escaping when they are most vulnerable early in life, but may not allow spatial or temporal flexibility to new or changing circumstances. However, if a species is, for example, preyed on by an especially dangerous predator and postattack survival is highly unlikely, the advantage of showing appropriate initial behaviour will clearly outweigh the disadvantage of a lack of plasticity.

Most studies showing seemingly unlearned predator recognition have been on species where young live independently from the moment of hatching (e.g. Brown & Warburton 1997; Burger 1998; Göth 2001). However, in those with parental care, it often appears as if individuals come to recognize predators over time (Maloney & McLean 1995; Hanson & Coss 1997; Griffin et al. 2000, 2001). The consistent pattern from these studies is that cues from experienced conspecifics trigger learning about predators (Griffin et al. 2000). Behaviour that requires time to perfect may result in an increased chance of errors when a predator is first encountered, but allows fine tuning to particular conditions: individuals can adjust their behaviour if predation risk varies in space and time, if they become exposed to previously unfamiliar predators, or if vulnerability to predation alters with age (Lima & Dill 1990; Warkentin 1995; Berger et al. 2001).

Compared to the development of predator recognition, very few studies have so far been conducted on the development of alarm call usage (see Table 1), but they have all reached similar conclusions. As with other call types (see e.g. Seyfarth & Cheney 1986; Hauser 1989), young seem predisposed from birth to use specific alarm calls in generally appropriate contexts, but they often give them to a broader range of species than adults (Seyfarth & Cheney 1980; Hollén et al. 2008). One possible explanation for this is that smaller individuals are preyed on by more predator types than adults and so young are using alarm calls in a way that is appropriate for their developmental stage (see Owings & Morton 1998). By alarm calling to a predator that threatens them, but not adults, young may be attempting to elicit a response that benefits the caller but that has no direct immediate benefit to the receiver; the alarm call is not necessarily acting as a warning to enhance the adult receivers' own safety. To date, only one study has provided suitable empirical data to test this assessment–management prediction. Hollén et al. (2008) compared the predator species that elicited alarm calls from meerkats of different ages and found that stimuli posing a greater threat to young than to adults do not elicit more calling from the former. These findings argue against age-related changes in vulnerability as the sole explanation for developmental changes in alarm call usage, at least in this species.

Rather than being age adaptive, young might alarm call to a greater number of species than adults because they make more errors. For example, Seyfarth & Cheney (1980) showed that alarm calls normally given by adult vervet monkeys to threatening stimuli are often uttered by young in response to nondangerous stimuli, such as doves (*Streptopelia* sp.), falling leaves or warthogs, *Phacochoerus africanus*, although these overgeneralizations are not entirely random: infants give 'leopard' alarms primarily to terrestrial mammals, 'eagle' alarms to objects in the air, and 'snake' alarms to snakes or long thin objects on the ground. As they grow older, vervets restrict their calling to particular predator species within these general classes. Although little is known about the neurological basis of alarm calling (see above), it could be that the increased vulnerability of young results in nervous systems and brain structures that are more sensitive to external stimulation than those of adults (Wiedenmayer 2009). The threshold for calling might therefore be lower in young, resulting in the production of alarm calls in contexts that would not elicit adult calling; development of adult-like call usage might therefore arise because of neurological maturation.

Alternatively, adult-like call usage might develop through increased experience with predator encounters and the alarm calls of others: individuals could learn to make fewer mistakes and become better at conveying the correct information. By hearing others use specific calls only in certain contexts, young could learn by association. There is also some evidence that adults might reinforce correct alarm call usage by juveniles. For example, adult vervet monkeys are more likely to give second alarm calls when infants alarm call to known predators than to nonpredators (Seyfarth & Cheney 1980), although no data are available on whether this leads to more rapid development. Moreover, if reinforcement does play a role, it may be inadvertent from an adult's perspective because they are equally likely to give second alarms following a correct alarm call by another adult as they are following a correct alarm call by a juvenile (Seyfarth & Cheney 1986). So, while adult responses may facilitate learning of correct alarm call usage, adults do not appear actively to teach infants in this context (Thornton & Raihani 2008).

Although there is some evidence for the involvement of learning, more studies are needed to determine the extent to which it drives the development of alarm call usage. In this regard, cross-fostering of young could be important. Research into the use of nonalarm calls by rhesus, *Macaca mulatta*, and Japanese, *Macaca fuscata*, macaques found that the normal striking species difference in calling was generally retained by cross-fostered individuals: they mostly adhered to their own rather than their adopted species' call usage, suggesting a strong unlearned component to this behaviour (Owren et al. 1993). To date, cross-fostering studies of alarm call behaviour have focused solely on the development of responses (see below). However, it is a method that could easily be used to tease apart the processes affecting the development of alarm call usage, especially in combination with call playbacks or presentations of live predators, stuffed models or predator deposits, such as urine, faeces and hair (see Kullberg & Lind 2002; Hollén & Manser 2007b). In general, the use of such experiments also provides an excellent means of increasing the sample size for infrequently and randomly occurring events, one of the problems with studying alarm call behaviour in natural populations.

DEVELOPMENT OF ALARM CALL RESPONSES

Young of many species respond to alarm calls seemingly on their first exposure to them. For example, only 24 h posthatching, mallard ducklings, *Anas platyrhynchos*, show a high degree of freezing upon hearing maternal alarm calls (Miller & Blaich 1986).

Similarly, on their first day of emergence from the natal burrow, juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, respond to ultrasonic alarm calls by increasing their vigilance (Wilson & Hare 2006), and juvenile Belding's ground squirrels enter the burrow or freeze when they hear conspecific alarm calling (Mateo 1996b). Such responses might be a simple consequence of the inherently positive acoustic properties of alarm calls (see Development of alarm call production). Alternatively, because an early ability to respond appropriately to alarm calls increases the likelihood of survival, and trial-and-error learning in a predatory context can be fatal, there should have been strong selection pressure for unlearned responses to alarm calls (Lind & Cresswell 2005). Young animals may therefore be born with the capacity to respond appropriately to alarm calls because evolutionary processes have fixed these traits in their behavioural repertoire (Blumstein 2006).

The exact response to alarm calls need not, however, remain fixed throughout life: in many species, changes in behaviour become apparent over a period of days, weeks or even months (Seyfarth & Cheney 1986; Mateo 1996b; Fischer et al. 2000; McCowan et al. 2001; Platzen & Magrath 2005; Hollén & Manser 2006; Fichtel 2008). For example, in the few days after first emergence from the burrow, juvenile Belding's ground squirrels become more selective and begin to respond more distinctly to alarm calls compared to nonalarm calls, to which they initially react in the same way. Three weeks later, their behaviour has further changed, although compared to adults they still freeze less, stay alert longer and run to the burrow more often (Mateo 1996b). In meerkats, young pups flee to a burrow in response to all alarm calls, but later respond differently depending on the urgency of the threat (Hollén & Manser 2006). Natural selection may favour unspecific responses early in life when avoiding predation is of paramount importance (food is provided by others), but refinement is needed to minimize the cost of unnecessary time and energy expenditure later in life: if the threat is not imminent, valuable foraging time will be lost by running to a burrow (Sih 1997; Lima 1998). Even seemingly unlearned responses may therefore be reorganized during development (Wiedenmayer 2009).

One possible explanation for a change in alarm call responses with increasing age is a change in vulnerability. For example, young white-browed scrubwren, *Sericornis frontalis*, nestlings are at risk from ground predators, but aerial predators pose little danger to them inside their enclosed nest. This might explain why young nestlings only suppress their calling in response to the playback of alarm calls signalling the presence of a ground predator, but not those signifying an aerial threat; the responses of nestlings are age adaptive (Platzen & Magrath 2005). Supporting this idea, the same authors later showed that scrubwren fledglings, which are at risk from aerial predators, fall silent immediately after playback of their parent's aerial alarm calls (Magrath et al. 2006). The development of responses to aerial and ground alarm calls in these birds shows striking similarities with the development of responses to such alarm calls in ground squirrels and mongooses (Mateo 1996b; Hanson & Coss 1997, 2001b; Hollén & Manser 2006), suggesting that age-adaptive developmental trajectories may be widely applicable across a broad range of species (see Alberts & Cramer 1988; Owings & Morton 1998).

An alternative explanation for differences in alarm call responses by individuals of different ages is that responses of young are not fully functional early in development. One reason for this might be constraints imposed by immature sensory or motor systems. For example, young red deer, *Cervus elaphus*, calves are limited in their capacity to run because of their low body weight: until their physical development reaches a certain point, they may be forced to respond to alarm calls by becoming immobile, rather

than fleeing (Espmark & Langvatn 1985). Brain areas such as the amygdala, the hippocampus and the prefrontal cortex, which form the 'fear circuit' and support defensive behaviour in general, may also lack full functionality early in life (reviewed in Wiedenmayer 2009). During development, new neurons will generate and differentiate (Berdel & Morys 2000), synaptic transmissions will change (Thompson et al. 2008), connections between different brain areas will mature (Rinaman et al. 2000), and hormones that are important for the activation of the fear circuit will be secreted (Moriceau et al. 2006). Although the consequences of neurological development on alarm call behaviour are poorly understood, it is highly plausible that these changes could alter the functional output of the fear circuit, and thus alarm call responses, by promoting or inhibiting certain behaviours. Processes independent of a direct interaction with either the predatory threat or alarm calls themselves can therefore contribute to differences in responses between age groups.

Although some changes in alarm call responses with age might be the result of unfolding maturation, early experience may also shape the behaviour of young by influencing the development of their perceptual, central or motor systems. There is good evidence that both social experience (Arakawa 2007) and maternal care (Champagne & Curley 2005) influence general defensive behaviour in juveniles, and both could feasibly play a role in the development of alarm call responses. For example, rearing conditions have been shown to affect the development of alarm call responses in rodents, with captive juvenile Belding's ground squirrels more likely to run to a refuge and to stay alert for longer than those raised in the wild (Mateo & Holmes 1999a). Moreover, captive-reared young started discriminating between different alarm calls later in life compared to their wild counterparts, and the authors suggested this was because pups in captivity were exposed to higher levels of auditory stimulation in their burrows. The permanent absence of mothers after weaning also delays the point at which wild juvenile Belding's ground squirrels respond differently to alarm and nonalarm calls (Mateo & Holmes 1997). However, future studies need to disentangle the importance of missing maternal care from a lack of opportunities for social learning (see below).

Young animals might also become more adult-like in competence, making fewer mistakes and responding more appropriately to alarm calls, through learning. Animals can learn how best to respond through direct interaction with alarm calls and predatory situations, but such individual learning is potentially costly (Griffin 2004). The risks can be minimized by using information from experienced companions. Such social learning is common in many species when it comes to predator recognition (Cook & Mineka 1990; Griffin 2004; Shier & Owings 2007), and is also likely to play a major role in the development of alarm call responses. For example, during the first 3 months of age, meerkat pups mostly run to the nearest adult when hearing an alarm call and can therefore observe and follow the responses of the more experienced individuals (Hollén & Manser 2006). Those pups that do not run to an adult are more likely to show adult-like responses if they first look at an adult individual (see also Seyfarth & Cheney 1986; Fichtel 2008). In general, there is a strong tendency for young to start responding in an adult-like fashion independently of others only when they begin spending time away from adults (McCowan et al. 2001; Hollén & Manser 2006; Fichtel 2008).

Given that experience with social companions is evidently important, there have been surprisingly few attempts to investigate the extent to which learning is involved in the development of alarm call responses. As with the study of alarm call usage, cross-fostering is likely to be particularly beneficial in this regard, but Davies and colleagues are the only researchers who have so far

attempted this with respect to alarm calls. In one study they cross-fostered newly hatched dunnocks, *Prunella modularis*, and robins, *Erithacus rubecula*, and revealed that both species cease begging only in response to conspecific alarm calls; they did not develop this response to their foster species' alarms, suggesting a strong genetic basis (Davies et al. 2004). The response of cross-fostered nestlings to conspecific calls was nevertheless weaker than that of nestlings raised by their own species, showing that some learning is necessary to fine-tune their natural responses (see also Madden et al. 2005; Davies et al. 2006). Although cross-fostering is likely to be easier in birds, studies on macaques have shown that it should not be discounted as a possibility with certain mammals (see Owren et al. 1993; Seyfarth & Cheney 1997).

There has also been little work on how neuroendocrine changes can affect responsiveness and learning in young animals. Studies comparing developmental trajectories and response behaviours of animals with different rearing histories would be invaluable in this regard because early social experience is known to affect neural development in the brain (e.g. Bredy et al. 2003), and particularly the molecular and cellular organization of the fear circuit (see Wiedenmayer 2009). Comparative research of this nature would also enable an investigation of the extent to which auditory experience is needed for alarm call response development. To date, only one such study has been conducted. Hauser (1988) compared wild populations of the same species that were exposed to different levels of alarm calls and predators and found that infant vervet monkeys exposed to high rates of superb starling *Spreo superbus*, alarm calls respond correctly to these calls earlier in development than individuals exposed to calls at a lower rate. If such comparisons are not feasible because variability in exposure is either lacking or difficult to quantify, some viable alternatives include providing groups of captive juveniles with different exposure levels (see Mateo 1996a), comparing wild and captive populations of the same species (although such different environments may confound the results; Mateo & Holmes 1999a, b; Hollén & Manser 2007b), or examining the behaviour of individuals in populations before and after the introduction of novel predators or the reintroduction of absent predators (Gil-da-Costa et al. 2003).

FUTURE DIRECTIONS

Despite the recent rapid increase in studies examining the development of alarm call behaviour, there is still much that remains unknown or unexplored. In addition to the suggestions detailed above, the following topics have the potential to provide particularly fruitful insights. First, all research on the development of alarm call production has so far been conducted on nonhuman primates and sciurids (see Table 1). This is particularly surprising given the vast research literature on the development of birdsong (reviewed in Catchpole & Slater 2008), and it is a shame that alarm calls were never considered by isolation studies investigating avian vocal development (e.g. Thorpe 1958; Morton et al. 1986; Hultsch & Todt 1992). Whereas song development clearly involves learning (Catchpole & Slater 2008), mammalian alarm calls seem to undergo relatively minor modification during development (Blumstein & Munos 2005; Randall et al. 2005; Hollén & Manser 2007a). Where do bird calls fit in? Does their development follow the same pathway as that of song or is it more similar to that of mammalian alarm calls, thus being guided by similar processes across taxa? Studies on the development of alarm call production in birds should be easy to initiate because the required techniques, such as the use of sophisticated acoustic analysis software, predator presentations and cross-fostering, are already well established. Moreover, the methods used to determine the neurological basis of birdsong could be easily transferred to studies of alarm calls, thus

providing a novel insight into their development in this taxa and more generally.

Second, although it is clear that learning is important for the development of alarm call behaviour, especially usage and responses, little work has attempted to tease apart the variety of individual and social processes that might be involved (see Janik & Slater 2000; Moore 2004; Dugatkin 2008). A few early studies that tackled this issue reared young of social species in total isolation (e.g. Herzog & Hopf 1984), but this method is ethically unsound and leads to questionable conclusions because the individuals involved are likely to display unnatural behaviours. To avoid these problems, we suggest instead the use of temporary removals at different ages. The isolated individuals could then be subjected to playbacks of alarm calls or model predator presentations and if, for example, they show appropriate responses, it suggests that they have developed an association between an alarm call and a particular response and/or context, rather than using cues given by adults or the sight of predators (the development of alarm call usage could be investigated in the same way). We also suggest that more simple learning processes should not be ignored. For example, young could cease responding to harmless stimuli through habituation, where repeated exposure causes a decline in responsiveness because no reinforcement follows (Thorpe 1963). Finally, it is worth noting that development need not be constrained to young animals: individuals may continue to adjust their behaviour throughout life, to changing circumstances. Different forms of learning may play a role at different times, but this possibility has received no research attention to date (Janik & Slater 2000).

The third major area we suggest for future consideration is the use of false alarm calls (given when there is no imminent danger) to gain an advantage in competitive interactions over food: if the victim responds by fleeing to cover, the alarm caller can potentially steal the food (Munn 1986; Ridley & Raihani 2007; Wheeler 2009). Frequent false calling by kleptoparasites is likely to reduce their effectiveness and the best rate might depend on, for example, the particular habitat and thus the ease with which receivers can identify whether a predator is actually present (Munn 1986). Young kleptoparasites therefore need to learn at what rate to give true and false alarm calls to be successful, but no studies have considered how this behaviour develops. To minimize the cost of responding to false alarm calls, host young also need to learn which heterospecific species give false alarm calls, the rate at which they do so and hence their relative level of unreliability, but how they do this has yet to be explored. How members of one species assess the reliability of individuals of another species would potentially help us understand the cognitive abilities underlying response behaviour and the flexibility of specific learning processes.

CONCLUSIONS

In general, there are strikingly different developmental trajectories for the different aspects of alarm call behaviour. Alarm call production undergoes relatively minor modification during development, appearing almost adult-like on first expression, and those changes that do occur are likely to be the consequence of physical, physiological and/or neurological maturation. In contrast, alarm call responses often undergo more dramatic changes as individuals grow older, and are more influenced by individual and/or social experiences gathered during development. Alarm call usage appears intermediate, with its development dependent on a mix of genetic predispositions, neurological maturation and/or experience. Perhaps because of the ease with which playback experiments can be conducted to test for differences in alarm call responses between adults and young, the majority of developmental studies have focused on this aspect of alarm call behaviour.

However, given that call production, usage and responses are controlled by different causal mechanisms, detailed examinations of all three aspects in the same species (so far only done in meerkats and vervet monkeys; Table 1) are vital.

Different species also vary greatly in the speed with which they develop alarm call behaviour. In terms of alarm call responses, for example, appropriate behaviour is apparent in some on first exposure to danger, while in others it can take months before such behaviour emerges. One reason for this is the sensitivity of behavioural development to local environmental conditions, which makes adaptive sense if factors that influence survival and reproduction differ from place to place or over time. Some differences between species in the pattern of their developmental trajectories might therefore be attributable to, for example, variation in the intensity of predation experienced by young animals. The amount of parental care provided is also likely to help explain interspecific differences in developmental rates. For example, in those species in which response patterns emerge over a long time, young seem to converge on adult-like responses at approximately 6–7 months. These species have in common that young are initially protected by their mothers or other adults, and the expression of adult-like behaviour seems to coincide with the point at which they start to move around independently. Sufficient studies have potentially been conducted on alarm call responses (although not the other two aspects of alarm call behaviour) to consider meta-analyses, thereby enabling us to acquire more powerful estimates of the true effect sizes for the influence of such variables as age and social experience.

Although it is very possible that in many cases the difference in behaviour between juveniles and adults is because the former have yet to acquire adult-like competence, it is equally plausible that their behaviour is age adaptive and subsequent changes are the result of, for example, a change in vulnerability or mobility. It is therefore important that the results of studies investigating the development of alarm call behaviour are subjected to interpretations from both the information transfer perspective and the assessment–management viewpoint. It is also worth noting that if we are interested in perceiver psychology, the assessment–management framework puts much more emphasis on this than the information transfer viewpoint; aspects of acoustic structure that, for example, increase or decrease detectability, discriminability and memorability all become more relevant in the former view. Although the two frameworks are by no means mutually exclusive, it would be possible in many cases to set up competing hypotheses to try to tease them apart. This does, however, require experimental studies of the survival value of specific behaviours, something that is currently lacking in the literature. By elucidating whether young behave in a way reflecting ontogenetic adaptations or preparation for maturity, as well as broadening the use of various techniques (e.g. cross-fostering, temporary removals), forming stronger collaborative links with other disciplines (e.g. physiology, neurobiology) and initiating new avenues of research (e.g. kleptoparasitism), research into the development of alarm call behaviour will continue to play a key role in our understanding of a wide variety of topics, including the evolution of communication and language, kin selection and cognitive processing.

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