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ORIGINAL PAPER

Ontogenetic changes in alarm-call production and usage in meerkats (*Suricata suricatta*): adaptations or constraints?

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Abstract In many species, individuals suffer major mortality in their first year because of predation. Behaviours that facilitate successful escape are therefore under strong selection, but anti-predator skills often emerge gradually during an individual's early development. Using long-term data and acoustic recordings of alarm calls collected during natural predator encounters, we aimed to elucidate two largely unsolved issues in anti-predator ontogeny: (1) whether incorrect predator assignment is adaptively age-appropriate, given that vulnerability often changes during development, or whether age-related differences reflect true mistakes made by immature individuals; and (2) the extent to which the development of adult-like competence in alarm-call production and usage is simply a function of maturational processes or dependent upon experience. We found that young meerkats (*Suricata suricatta*) were less likely to give alarm calls than adults, but alarmed more in response to non-threatening species compared to adults. However, stimuli that pose a greater threat to young than adults did not elicit more calling from young; this argues against age-related changes in vulnerability as the sole explanation for developmental changes in calling. Young in small groups, who were more likely to watch out for predators, alarmed more than less vigilant young in larger groups. Moreover, despite similarities in acoustic structure between alarm call types, calls appeared in the repertoire at different rates, and those that were associated with frequently encountered predators were produced relatively early on. These results indicate that experience is a more plausible explanation for such developmental trajectories than maturation.

Keywords Meerkats · Alarm calls · Development · Experience · Maturation · *Suricata suricatta*

Introduction

Many species of birds and mammals give alarm calls to warn others of danger (Klump and Shalter 1984), and in several species, these calls provide accurate information about the type of predator approaching, the urgency of the threat or both (Macedonia and Evans 1993; Manser 2001). Although we might expect individuals to be born with the ability to extract such information, appropriate anti-predator skills often emerge gradually during early development (e.g. Seyfarth and Cheney 1980, 1986; Mateo 1996a, b; Ramakrishnan and Coss 2000; McCowan et al. 2001; Platzen and Magrath 2005; Hollén and Manser 2006, 2007). Infant vervet monkeys (*Cercopithecus aethiops*), for example, frequently give alarm calls to non-threatening stimuli, but over time come to restrict their calls to the species that prey on them (Seyfarth and Cheney 1980). Whether more liberal predator assignment by young is

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adaptively age-appropriate, given their greater vulnerability, or is simply over-generalization that is narrowed by honing, is an open question.

Whether the gradual development into adult-like competence is simply a function of physical maturation, with immature sensory, perceptual or motor systems unfolding on their own, or of exposure/experience also remains uncertain. A large number of studies on a variety of different species, most of them focusing on how young respond to alarm calls, suggest that experience does play a crucial role (reviewed in Griffin et al. 2000). For instance, vervet monkeys exposed to superb starling (*Spreo superbus*) alarm calls at high rates respond correctly to these calls earlier than individuals exposed at a lower rate (Hauser 1988). Experience with the behaviour of adult group members can also enhance the specificity of juvenile responses (Seyfarth and Cheney 1986) or cause correct responses to develop more quickly (Mateo and Holmes 1997). Yet, despite abundant evidence in favour of experience as a cause of skill development, it is difficult to discard completely the role of maturation (e.g. Hollén and Manser 2006). Furthermore, whereas the responses to alarm calls have been frequently examined, far less attention has focused on how the honing of anti-predator skills is achieved in the two other domains of vocal development, i.e. the production and correct usage of alarm calls.

In this study, we examined the developmental trajectories of alarm-call production and usage in meerkats (*Suricata suricatta*) and aimed to disentangle the effects of risk-sensitivity vs perceptual honing and the relative importance of maturation and experience. Meerkats provide a particularly tractable study system to address these issues. They are small, cooperatively breeding mongooses which are preyed on by a variety of raptors, mammals and snakes (Clutton-Brock et al. 1999a). Young individuals in particular suffer from a high (approximately 30%) mortality rate due to predation (Doolan and MacDonald 1997). Meerkats frequently give alarm calls and exhibit a sophisticated system in which certain calls are given only in response to specific predator types (for example, raptors), while calls given to a close predator are structurally different from those given to the same predator at further distances (Manser 2001). Moreover, meerkats also emit calls which are unrelated to a single predator type (for example, sudden disturbances; Manser 2001). Our study population consists of several well-habituated groups, representing a unique opportunity to follow large cohorts of mammals throughout their development.

We used behavioural observations of naturally occurring predator encounters to investigate: (1) whether the rate of alarm calling changed with age; (2) the type of stimuli to which young and adults gave alarms; (3) the type of alarm calls that were used at different ages; (4) whether calls were used correctly; and (5) whether exposure rate might influence calling in young. If alarm calling by young reflects their greater vulnerability, they should call more frequently than adults to stimuli posing a greater threat to young than adults. If, however, honing of skills is required, young would call less than adults, but call proportionally more in response to non-threatening stimuli. If maturation is more important than experience, alarm calls with similar acoustic structure would appear simultaneously in the vocal repertoire, and differences in the exposure rate of different stimuli should have little effect. If experience plays a major role, alarm calls may appear gradually in the repertoire, and young should produce more of the alarm calls that correspond with the adult alarm calls that they hear the most and/or with the predator type they encounter most frequently. Because attentive individuals may more easily detect predators (Gaston 1977) and hence be more likely to emit alarm calls (Manser 1998), we also investigated whether young and adults differed in their vigilance behaviour. If a lack of alarm calls is due to a lack of vigilance, and is therefore a consequence of experience rather than maturation, we predicted that vigilance would directly correlate with alarm calling in young.

Materials and methods

We collected data on a population of wild, but habituated, meerkats near VanZyl's Rus in the South African part of the Kalahari Desert (26°58′S, 21°49′E; details of study site provided in Clutton-Brock et al. 1999a). Animals were habituated to human presence and non-invasively marked for individual identification with hair dye or hair cuts applied to their fur, allowing detailed observation of particular individuals from within 1 m. The open habitat makes simultaneous monitoring of several individuals easy. Ages of all individuals were known because they had been monitored since birth. Pups were defined as animals younger than 3 months, juveniles as 3–6 months, subadults as 6–12 months and adults as older than 12 months. Individuals less than 12 months are collectively referred to as 'young' on some occasions.

Rate of alarm calling and vigilance

To investigate age differences in the rate of alarm calling, we used data from the long-term database of the Kalahari Meerkat Project on the identity of individuals calling during natural predator encounters. These observational data have been collected by a team of researchers for 11 years. For our analyses, we randomly chose one litter from ten different groups, born between 2000 and 2002. For the first year of each litter's life, we extracted all alarm calls emitted by young (mean number of young per group ranged from 3 to 5) belonging to the chosen litter and all adult group members (mean number of adults per group ranged from 3 to 20). To control for the amount of time spent with each group, we extracted the number of hours that groups were observed on those days when alarm calls were given. We only included days when a group was observed for 1 hour or more. We extracted a total of 946 days on which alarm calls were given (range 58–116 days per group), encompassing calls from 42 young (19 females and 23 males) and 167 adults (78 females and 89 males). Half of the young individuals were sampled repeatedly as pups or juveniles and later as sub-adults (range 73–299 days in between samples).

To gauge the effect that vigilance has on the rate of alarm calling, we extracted all events where young and adult individuals in the same ten groups and over the same time periods as above acted as sentinels (scanning for predators from a raised position, hereafter referred to as guarding; Clutton-Brock et al. 1999b). Additionally, because foraging meerkats also frequently scan for predators, we investigated age differences in this behaviour (hereafter referred to as scanning). Because such scanning is not recorded in the long-term database, we collected these data using a focal sampling procedure (Altmann 1974). Randomly selected focal individuals were followed for 20 min during which we recorded the number and length of scanning bouts on a Psion Organiser II (Psion Teklogix, Ontario, Canada). Each individual was used as a subject only once. We conducted focal watches on 12 pups (7 females and 5 males), 23 juveniles (13 females and 10 males), 16 sub-adults (10 females and 6 males) and 18 adults (11 females and 7 males) in 11 different groups during 2003 and 2004.

Use of alarm calls

1. What stimuli do young and adults alarm at?

To examine whether young individuals alarm at a wider range of stimuli than adults, we investigated what type of aerial stimuli elicited calls. We restricted it to aerial contexts because the majority of terrestrial encounters were with non-dangerous stimuli posing little threat to both young and adults and encounters with snakes occurred too rarely to be included. We classified aerial stimuli into three broad categories: small raptors (e.g. pale-chanting goshawks, *Melierax canorus*), large raptors (e.g. martial eagles, *Polemaetus bellicosus*) and non-threatening birds, including vultures (e.g. white-backed vultures, *Gyps africanus*) and smaller birds (e.g. yellow-billed hornbills, *Tockus leucomelas*). Although birds in the last category pose no threat, they sometimes elicit alarm calls. Both young and adults can fall prey to large raptors, whereas small raptors are more likely to take young (Clutton-Brock et al. 1999a). We extracted a total of 979 alarm calling events by juveniles ($N=35$), sub-adults ($N=194$) and adults ($N=750$) in the same ten groups as above. Pups were excluded because of low sample size.

2. What types of alarm calls are produced and are they used correctly?

To investigate what types of alarm calls are produced by young, when they appear in the repertoire and whether they are used in the correct context (data which are not available in the long-term database), we analysed natural alarm calls recorded between 2003 and 2005 by LIH and an additional observer. Alarm calls were recorded ad libitum using a Sennheiser directional microphone (ME66/K6 with a MZW66 pro windscreen; Old Lyme, CT, USA) connected to a Sony digital audio tape recorder DAT-TCD D100 (Sony, Tokyo, Japan) or a Marantz PMD-670 solid state recorder (D&M Holding, Kanagawa, Japan). The identity of individuals giving alarm calls and the type and distance to the stimuli evoking them were spoken onto the tape. Recordings were digitally transferred to a PC, and calls were identified and classified based on their acoustic structure (Manser 2001; see also Fig. 1).

We identified three classes of calls specific to particular predator types (hereafter referred to as predator-specific): aerial, terrestrial and recruitment calls. Aerial calls were given either in response to raptors or to non-threatening birds. Terrestrial calls were mostly given to mammals, threatening or non-threatening, approaching on the ground. Recruitment calls were given to snakes and to deposits of faeces, urine or hair of foreign meerkats or predators. All three call classes were further classified into two urgency levels, resulting in six different call types (Table 1). Deposits and stimuli at a far distance elicited low urgency calls, whereas snakes (and sometimes deposits) and stimuli at a close distance elicited high urgency calls (Table 1). In addition to predator-specific alarm calls, we also distinguished between six call types emitted in contexts not specifically related to a single predator type (hereafter referred to as non-specific; Table 1). We classified a total of 325 calls from young and 298 from adults in 13 groups.

When investigating the use of these alarm calls, we only included the recorded calls for which we knew the exact eliciting stimuli. Because it is often difficult to identify reliably the cause of an alarm, sample sizes were greatly reduced ($N\text{young}=51$, $N\text{adults}=95$). Stimuli were classified as raptors (small and large), non-threatening birds and terrestrial. Recruitment events were excluded because of low sample size. Because non-specific calls were given in response to a number of different stimuli, we only classified predator-specific calls as correct or wrong ($N\text{young}=19$, $N\text{adults}=54$). To ensure that we provide a reliable estimate of the rate at which young and adults give inaccurate calls

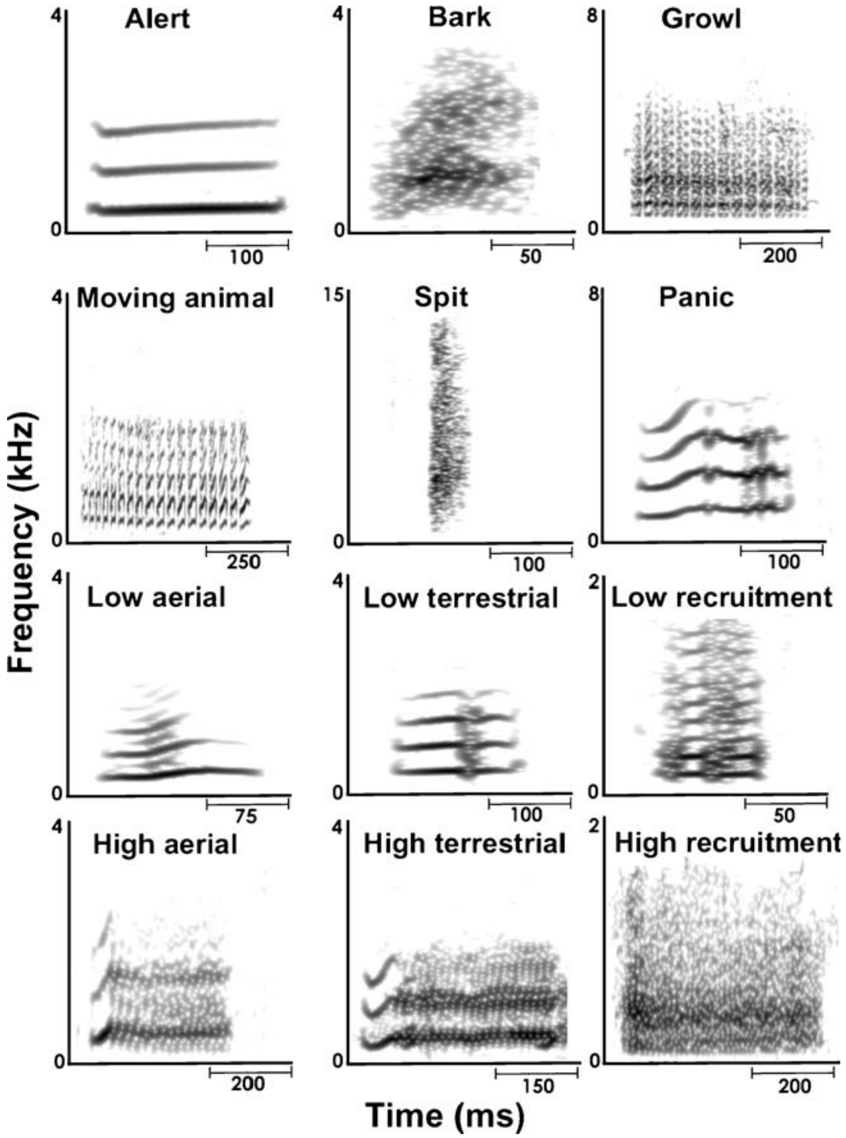

Fig. 1 Spectrograms of the 12 call types included in the analyses (see Table 1 for description). Low and high refers to urgency levels

given the small sample sizes, we compared the results to those obtained when sample sizes were increased (Nyoung= 44, Nadults=76) by including additional behavioural data (alarm calls and stimuli evoking them) that had been simply noted down, but not recorded on tape.

Encounter rate of different stimuli

To investigate whether alarm calling in young might depend on the frequency with which different stimuli are encountered, we extracted (from the long-term database) the number of aerial and terrestrial stimuli encountered over a 1-year period in six of the ten groups sampled above. Recruitment events were excluded due to the difficulty of getting a large enough sample size. We included a total of 713 days when encounters occurred (range 75–141 days per group). Each group had been observed for a mean of 3.2 h per day (range 3–3.4 h per group).

Statistical analyses

We conducted all analyses in R for Microsoft Windows version 2.4.1 (R Development Core Team 2006) using the software packages ‘MASS’ (Venables and Ripley 2002) and ‘nlme’ (Pinheiro et al. 2005). We analysed the proportion of days on which different age classes were observed alarm calling and the rate of calling each day (both weighted for the time spent observing each group) using an analysis of variance (ANOVA) with the mean values per age class and group as response variables. The proportion of days on which each age class guarded, and the rate of guarding per day (both weighted for the time

Table 1 Description of the six predator-specific (given to particular predator types) and six non-specific (unrelated to particular predator types) alarm calls included in the analyses

	Call type	Urgency	Context
Specific	Low aerial	Low	Raptors far away (>200 m)
	High aerial	High	Raptors close (<200 m)
	Low terrestrial	Low	Herbivores/ground predators far away (>50 m)
	High terrestrial	High	Herbivores/ground predators close (<50 m)
	Low recruitment	Low	Deposits such as faeces or hair
	High recruitment	High	Snakes/deposits
Non-specific	Alert	Low	Non-threatening birds close/raptors far away
	Moving animal	Low/high	Animals moving (raptors, mammals, non-threatening birds)
	Growl	Low	Mostly non-threatening stimuli (e.g. small birds) within a few meters of the caller
	Spit	High	Threatening (e.g. snakes) or non-threatening (e.g. small birds) stimuli within a few meters of the caller
	Bark	High	Raptors perched/circling closely or ground predators very close
	Panic	High	Sudden movements in close proximity or bird alarm calls

Growl calls were given by young only.

spent observing each group) was analysed with Kruskal–Wallis tests using the mean values per age class and group as response variables. We analysed the frequency and mean duration of scanning bouts on the ground as a function of age class using Kruskal–Wallis tests. Because group size influences both the rate of alarm calling (Manser 1998) and vigilance (Clutton-Brock et al. 1999b) in adults, we also investigated whether this is the case in young. We used ANOVAs with the mean number of calls per individual and the proportion of days guarding by young as a function of the mean number of adults present during the period of observation. A chi-square test was used to compare the distributions of alarm calls by juveniles and sub-adults with those that would be expected given the adult rate of calling to the same stimuli. The encounter rate of aerial and terrestrial stimuli was analysed using an ANOVA with the mean number of encounters per group and day as a function of stimuli type (weighted for the time spent observing each group).

Results

Rate of alarm calling and vigilance

The rate of alarm calling increased with increasing age (ANOVA: proportion of days alarm calling: $F_{3,36}=539.79$, $P<0.001$; hourly rate: $F_{3,36}=38.82$, $P<0.001$; Fig. 2). Only four pups (and these only after reaching 60 days of age) in three out of the ten litters were observed to give alarm calls. After reaching juvenile age at 3 months, individuals in seven litters were observed alarm calling, and by the time they reached sub-adult age at 6 months, individuals in all ten litters were consistently giving alarm calls. Young showed a higher rate of alarm calling each day when fewer adult individuals were present (ANOVA: $F_{1,118}=6.42$, $P=0.01$).

Both the proportion of days an individual was observed guarding and the number of guarding bouts per hour increased with increasing age (Kruskal–Wallis: proportion days: $\chi^2=25.52$, $df=2$, $P<0.001$; per hour: $\chi^2=20.88$, $df=2$, $P<0.001$; Fig. 3a). Pups were never observed

Fig. 2 Rate of alarm calling by individuals of different ages. **a** Mean (±SE) number of alarm calls given by pups (<3 months), juveniles (3–6 months), sub-adults (6–12 months) and adults (>12 months) per observation hour. **b** Number of calls per observation hour for each young individual during different stages in their development. Some of the young individuals were sampled repeatedly as pups or juveniles and later as sub-adults

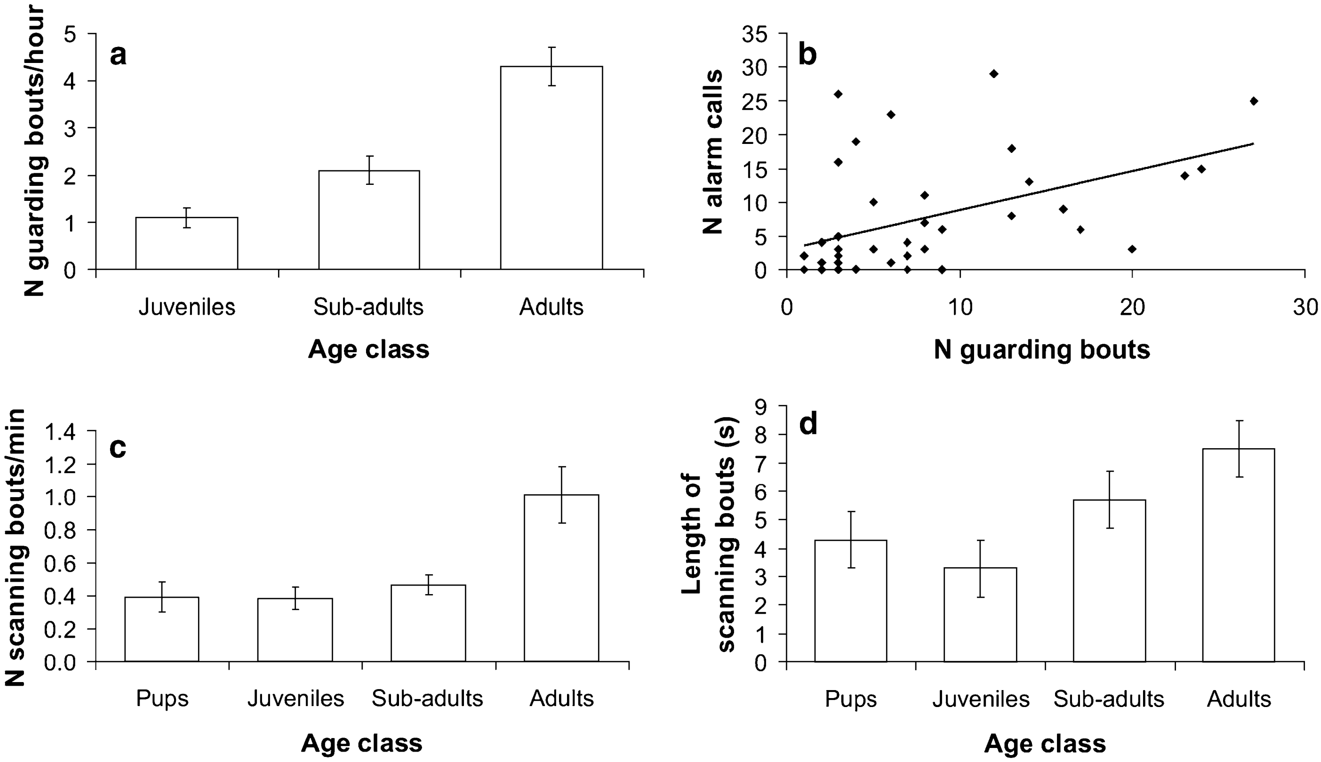

Fig. 3 Guarding and scanning by individuals of different ages. **a** Mean (±SE) number of guarding bouts per observation hour for juveniles, sub-adults and adults (pups were never observed on guard). **b** Correlation (with fitted linear regression line) between the number of alarm calls given by juveniles and sub-adults and the number of guarding bouts by the same individuals over a 1-year period. **c** Mean (±SE) number of scanning bouts per minute focal watch. **d** Mean (±SE) length of scanning bouts by foraging individuals

guarding, and, as with alarm calling, frequent guarding only began when individuals reached 6 months of age. Juveniles and sub-adults in small groups (<10 adults) were observed on guard more often than those in bigger groups (ANOVA: $F_{1,8}$=7.13, *P*=0.03). Moreover, the rate of calling was higher amongst those juveniles and sub-adults who guarded more (ANOVA: $F_{1,39}$=9.14, *P*=0.004; Fig. 3b). Compared to adults, young also scanned less frequently when foraging (number of scanning bouts: Kruskal–Wallis: χ^2=11.55, *df*=3, *P*=0.009; Fig. 3c), and adults tended to have longer bouts than young (Kruskal–Wallis: χ^2=6.36, *df*=3, *P*=0.10; Fig. 3d). The number of adults present did not influence the scanning behaviour of young (Kruskal–Wallis: *P*>0.30 for both variables).

Use of alarm calls

1. What stimuli do young and adults alarm at?

The distribution of alarm calls by juveniles and sub-adults differed to that of adults (chi-square test with six data/expectation pairs: χ^2=130.3, *df*=5, *P*<0.001; Table 2). Juveniles and sub-adults gave fewer alarm calls to large raptors than would have been expected had they distributed their alarms exactly like adults, whereas the distributions of calls to small raptors were equal to that of adults. Juveniles and sub-adults also gave more alarm calls to non-threatening bird species compared to adults.

2. What types of alarm calls are produced by young and are they used correctly?

The majority of alarm calls recorded from pups, juveniles and sub-adults were, in contrast to adults, non-specific (young 80%, *N*=325; adults 37%, *N*=298; chi-square test: χ^2=185.84, *df*=3, *P*<0.001; Fig. 4). Non-specific alarm calls, in particular growl calls (Table 1), were the only calls heard from pups within the first month of emergence (*N*=131), and more than 70% of the predator-specific alarm calls appeared after 3 months of age (*N*=64). Amongst the predator-specific calls emitted by young, low-urgency aerial calls were the most frequently heard calls (63%, Fig. 4).

Although only 4 out of the 19 predator-specific calls recorded from young individuals were emitted in the wrong contexts, this was more than the proportion of wrong calls given by adults (1 out of 54; Fisher's exact test: *P*=0.02). Three of the four calls were terrestrial calls given by young aged 67, 183 and 241 days in response to raptors, and one call was an aerial call given to a car passing by (pup aged 87 days). Because 30% (*N*=54) of all aerial-specific calls given by adults were in response to vultures, we did not classify aerial calls given by young in response to vultures

Table 2 Distribution of alarm calls by adults, sub-adults and juveniles

	Adults Count	Sub-adults	Juveniles
Large raptors	373	66 (97.4)	8 (17.4)
Small raptors	71	18 (18.6)	3 (3.3)
Non-threatening birds	306	110 (44.9)	24 (9.8)
Total	750	194	35

Values in brackets are the number of alarm calls expected by sub-adults and juveniles had they distributed their calls exactly like adults

(16%) as wrong. The proportion of wrong calls given by both young and adults remained similar when sample sizes were increased by including behavioural data (young, 7 out of 44 wrong; adults, 1 out of 76 wrong; Fisher's exact test, $P=0.01$).

Encounter rate of different stimuli

All groups encountered more aerial than terrestrial stimuli per day (mean±SD: aerial=2.4±2.5, terrestrial=0.8±1.1; ANOVA: $F_{1,10}=89.2$, $P<0.001$). Moreover, groups encountered more non-threatening vultures than raptors each day (vultures=1.0±1.7, raptors=0.5±1.0; ANOVA: $F_{1,10}=19.6$, $P=0.001$).

Discussion

One largely unsolved issue in the field of vocal development is whether differences between young and adults are adaptively age-appropriate, given that vulnerability often changes during development, or whether young are simply constrained because perceptual honing with age is required. If young are particularly vulnerable, they should be calling more frequently to stimuli posing a greater threat to them than to adults. Because young meerkats did not alarm more than adults to small raptors, which pose a greater threat to young than adults (Clutton-Brock et al. 1999a), vulnerability is insufficient as an explanation. Instead, our results suggest that the honing of skills may provide a more plausible explanation. Young meerkats, especially before 6 months of age, were less likely to give alarm calls compared to adults. Moreover, young gave fewer alarm calls to threatening large raptors than would have been expected given the distribution of adult calls. Finally, although adults regularly alarmed to non-threatening vultures, perhaps because of their great abundance, juveniles and sub-adults did so more often than adults; young made more mistakes than adults.

The fact that vultures resemble raptors may cause young to over-generalize. However, relatively old individuals also gave mistaken alarm calls; this makes it unlikely that young made mistakes because their perceptual systems were too immature to discriminate vultures from raptors. More research is therefore needed to establish the exact mechanisms behind such calling patterns. Irrespective of the process involved, however, if honing plays an important role in the development of correct call usage, it would be advantageous for young individuals to acquire quickly the associations between external stimuli and call types. This may be particularly important in predation contexts where giving correct alarm calls could ensure the safety of other group members. Although we did record more mistakes by young than by adults, the error rate was relatively low in both age classes. Thus, even if honing is required, restricting alarm calling to relevant stimuli does indeed develop rapidly. Although it has been suggested in non-human primates that correct use of alarm calls might be reinforced by subsequent calling by adults (Seyfarth and Cheney 1980), we have no evidence of such reinforcement in meerkats (personal observation).

Another unsolved issue in developmental studies is the extent to which honing of skills is achieved through maturation or experience. Several of our results show that experience with predators probably has the strongest influence on the developmental trajectories of alarm calling found in meerkats. Consistent with findings in many juvenile mammals (see Arenz and Leger 2000), young meerkats were much less vigilant than adults. Assuming that predator detection depends on the frequency with which individuals scan their surroundings (McNamara and Houston 1992), vigilant individuals would be more likely to detect predators and give subsequent alarms. Supporting this, both an earlier study on adult meerkats (Manser 1998) and this study on young individuals showed that alarm calling is correlated with guarding. Similar to adults (Clutton-Brock et al. 1999b), young also increased their guarding with decreasing group size, and young in small

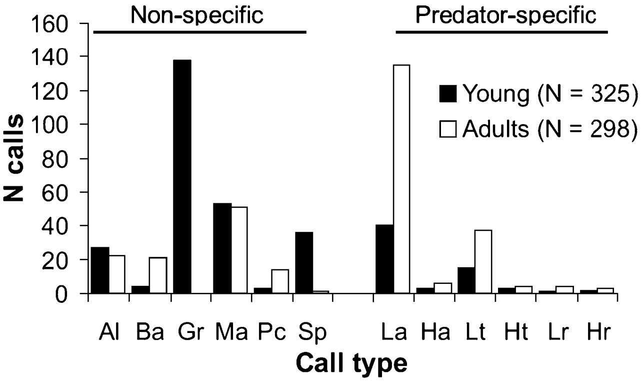

Fig. 4 The number of non-specific and predator-specific alarm calls given by young (pups, juveniles and sub-adults pooled) and adults. *Al* alert, *Ba* bark, *Gr* growl, *Ma* moving animal, *Pc* panic, *Sp* spit, *La* low aerial, *Ha* high aerial, *Lt* low terrestrial, *Ht* high terrestrial, *Lr* low recruitment, *Hr* high recruitment (see Table 1 for description of the different call types)

groups with few adults present alarmed more than young in larger groups. This shows that vigilance could play a role in determining alarm calling behaviour and that maturation alone is insufficient to explain such findings.

Alarm calls that are given specifically to particular predator types did not appear in the repertoire before young meerkats reached 3 months of age. Instead, unlike adults, most of the alarm calls recorded from young were non-specific calls given in response to several types of stimuli. It is possible that the non-specific alarm calls produced by meerkats, the majority of which are typically noisy in structure and therefore require relatively little control over the vocal apparatus (e.g. Lieberman 1986; Hammerschmidt et al. 2001; Scheiner et al. 2002), are easier for young to produce. Both maturation processes as well as training of muscular coordination can improve this control (Boliek et al. 1996). However, this does not explain why high-urgency predator-specific calls, also noisy in structure, appeared later in the repertoire. Moreover, the non-specific alert call is a tonal call similar in structure to the predator-specific low-urgency aerial call, but was produced within the first month of emergence. It is, therefore, unlikely that motor constraints alone explain the late appearance of predator-specific calls, and perhaps, experience plays an important role in the development of their vocal repertoire.

If young learn to produce alarm calls by experience rather than maturation, one would also expect them to produce more of the calls that correspond with the adult alarm calls that they hear the most and/or with the predator type they witness the most. Although experiments are needed to determine the precise role of auditory and/or perceptual experience in meerkats, we found that low-urgency aerial calls were most common amongst the predator-specific calls recorded from young individuals. Because aerial encounters occurred more frequently than terrestrial encounters and low-urgency aerial calls are by far the most commonly heard call type from adult meerkats at our study site (unpublished data), variable exposure to certain calls and predators may indeed be important.

To conclude, we show that meerkat young are capable of classifying events which are critical for survival. Despite that, however, adult-like skills in producing and using alarm calls develop over the first year of life. Our results do not support the idea that calling amongst young is the subject of developmental adaptation, but rather honing of alarm-calling skills seems required. Although we have provided some evidence suggesting that experience plays the most important role in such honing, the development of anti-predator behaviour is likely to be a complex phenomenon that relies on an interaction between maturational processes and learning, and it may be inappropriate to discard the role of either one (see also Hollén and Manser 2006). A learning process, however, could provide the relevant adjustments needed for dealing with specific predators perceived under variable levels of urgency. It is also hard to believe that selection would have favoured a complete reliance on the unfolding of a fixed developmental pattern in species where individuals are subjected to changing risks during development, and are frequently faced with several predator types evoking different alarm calls.

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