Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics

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(Received 24 July 2005; initial acceptance 28 September 2005; final acceptance 26 March 2006; published online 6 October 2006; MS. number: 8630R)

Given the strong selection on prey animals to escape predation, early development of correct avoidance strategies should be favoured. We studied the development of responses to conspecific alarm calls in a free-ranging population of meerkats in South Africa. Through behavioural observations of naturally occurring predator encounters and playback experiments, we monitored responses of young individuals from emergence (3 weeks) to 6 months of age and compared them with those of adults (> 12 months). Although the total proportion of responses differing from those of adults was low during the observed period, the probability of responding like adults increased with age. Female young, who remained in closer contact to adults than did male young, were also more likely to show adultlike responses. The largest proportion of non-adultlike responses was shown before reaching independence at 3 months of age, and during this time young commonly ran immediately to a nearby individual when hearing an alarm call. After playbacks of alarm calls, young also reacted more slowly, resumed foraging sooner and spent less time vigilant than did adults. We conclude that young may need experience during early development to associate an alarm call correctly with the type of threat and appropriate response. Older group members may also serve as indirect models, perhaps helping young to form this association.

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Animals are predisposed to learn about features in their environment that are relevant to their survival, but given the strong selective force that predation exerts on animals, in particular young individuals, one might expect avoidance strategies to be fully functional upon a first encounter with a predator. However, if predation risk varies in space and time (Lima & Dill 1990), or if an environmental change causes animals to be exposed to previously unfamiliar predators (Berger et al. 2001), learning would allow responses to be adjusted to local conditions. Furthermore, the protection of young from predators is an essential component of parental care (Clutton-Brock 1991), so the presence and form of parental care may influence the behaviour and survival of young. In species where parental care is present, young may rely on their parents to defend them against predators or have the opportunity to learn how to avoid them (e.g. Hodge 2003; Platzen & Magrath 2004), whereas young that do not receive parental care may be under higher pressure to have functional antipredator behaviour from birth (e.g. Impekoven 1976; Miller & Blaich 1986; Göth 2001).

Research on the development of alarm call responses in mammals has focused mainly on nonhuman primates (reviewed in Seyfarth & Cheney 1997) and ground squirrels (Mateo 1996a,b; Hanson & Coss 2001). In both nonhuman primates and ground squirrels, the appropriate responses to alarm calls seem to develop gradually with age, suggesting that young individuals need experience to associate alarm calls correctly with the type of threat and correct response. For example, infant vervet monkeys, *Chlorocebus* (formerly *Cercopithecus* aethiops), of 3–4 months of age rarely responded like adults, whereas most infants older than 6 months did so (Seyfarth & Cheney 1986). The need for experience was further supported by Hauser (1988), who found that infant vervet monkeys exposed to superb starling, *Spreo superbus*, alarm calls at a high rate responded appropriately to these calls at an earlier age than did infants exposed to these calls at a lower rate.

Given that learning how to avoid predators might be costly to acquire through individual experience, it is perhaps not surprising that there is substantial evidence for social influences on antipredator behaviour in a wide range of taxa, including fish, birds and mammals.
(reviewed in Griffin 2004). In addition to observational conditioning (Cook et al. 1985), where individuals acquire alarm responses to previously neutral stimuli, the exposure to alarm behaviour of conspecifics can also enhance the specificity of juvenile responses (Seyfarth & Cheney 1986) or cause correct responses to develop more quickly (Mateo & Holmes 1997).

In contrast to studies on human language development (e.g. Galsworthy et al. 2000; Berglund et al. 2005), differences in communicative skills between the sexes have received comparatively little attention in studies of animal vocal development (but see Gouzoules & Gouzoules 1989; Yamaguchi 2001). To our knowledge, studies on the development of alarm call responses have not looked specifically at sex differences between young. However, this question may be important in species where survival of young differs between the sexes, such as described for meerkats, where female pups were more likely to survive than male pups (Russell et al. 2002).

Meerkats provide an excellent opportunity to investigate how young individuals develop their antipredator skills. Pups, which are cooperatively reared by the group and remain below ground for approximately 3 weeks after birth (Clutton-Brock et al. 1999a), face extreme challenges during early development as they move from safety underground to a life above ground. First, meerkats live under high predation pressure and are preyed upon by several aerial and terrestrial predators, including snakes (Clutton-Brock et al. 1999b), so pups are suddenly exposed to a wide variety of predators and alarm calls given by older group members. Adults utter different alarm calls, eliciting different behavioural responses depending on predator type and the level of response urgency, allowing group members to respond appropriately to calls uttered in a specific context (Manser 2001; Manser et al. 2001). Young individuals, especially before reaching independence at 3 months of age, are particularly vulnerable and suffer from a high mortality rate (approximately 30%) from predation (Doolan & MacDonald 1997; Clutton-Brock et al. 1999b). Consequently, young should be strongly selected to respond appropriately at an early age.

Second, during the first 2 months of foraging with the group (age 4–12 weeks), pups depend mainly on other group members for food (Doolan & Macdonald 1999), and therefore stay very close to older individuals. Older pups, however, probably have to spend more time away from other group members because they must rely on their own foraging skills. Therefore, if pups use such information, this change in foraging behaviour during early development may also influence the acquisition and use of social information.

We investigated the development of alarm call responses based on observations of naturally occurring predator encounters and playback experiments. We concentrated on three issues. First, we examined whether the responses to alarm calls changed with age. Second, we investigated whether the responses of male and female young differed. Third, we examined the influence of proximity to adult individuals, the number of helpers relative to the number of pups and the number of nearby individuals.

**METHODS**

We studied the development of alarm call responses in 11 groups of free-ranging meerkats along the dry bed of Kuruman River in the southern part of the Kalahari Desert in South Africa (26°58’S, 21°49’E) from January to July 2003 and from October 2003 to June 2004 (details on study site provided in Clutton-Brock et al. 1999b). All animals were habituated to close observation (<1 m) and marked for individual identification with hair dye or hair cuts applied to their fur. These marks were small and were applied noninvasively during sunning at the morning sleeping burrow. 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. Pups and juveniles are hereafter referred to as young. The study was conducted with the permission of Northern Cape Conservation Service and the ethical committee of Pretoria University, South Africa.

**Behavioural Observations**

We collected longitudinal data on responses to naturally occurring alarm calls using an ad libitum sampling procedure (Martin & Bateson 1993). Whenever an alarm call was uttered, we noted the following observations on a Visor Pro handheld computer (palmOne, Inc., Milpitas, California, U.S.A.): (1) first response (within 2 s of the initial alarm) shown by the nearest young (one or several) in sight; (2) first response shown by at least half of all group members older than 6 months observed during the time of alarm (taken as a typical adult response). If no specific response was shown by more than half of the individuals, the most frequently occurring response was noted; (3) most extreme response (following the first response if response escalated) shown by young; (4) most extreme response shown by at least half of the older group members. If the response did not escalate, the most extreme response equaled the first response.

We classified responses as ‘look briefly’, ‘watch continuously’, ‘move’, ‘move to bolthole’, ‘move below ground’ or ‘mob’ (Table 1). If an individual’s behaviour did not change following an alarm call, it was scored as ‘not responding’. First responses where young looked up briefly

<table>
<thead>
<tr>
<th>Response code</th>
<th>Explanation</th>
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<tbody>
<tr>
<td>Look briefly</td>
<td>Look in the direction of threat for &lt;3 s</td>
</tr>
<tr>
<td>Watch continuously</td>
<td>Follow the threat, continuously observing it until it has passed by a bolthole</td>
</tr>
<tr>
<td>Move</td>
<td>Run but not all the way to a bolthole</td>
</tr>
<tr>
<td>Move to bolthole</td>
<td>Run to a bolthole mouth and stop</td>
</tr>
<tr>
<td>Move below</td>
<td>Flee down a bolthole</td>
</tr>
<tr>
<td>Mobbing</td>
<td>Gather around threat with erect fur and tail</td>
</tr>
</tbody>
</table>
or watched continuously were then classified as scanning the surroundings or looking towards another individual. Looking towards another individual was defined as the young clearly focusing on an individual nearby instead of continually moving its head to follow the threat. Responses where young moved a short distance, moved to a bolthole, moved below ground or mobbed were classified as first running up to another individual (within 0.5 m) or running independently for shelter or towards threat. Finally, responses where young responded independently of other individuals, i.e. did not look towards or run to another individual, were classified as adultlike (same response as adults) or non-adultlike (different response to adults). To investigate whether the non-adultlike responses still resembled those of adults or if they differed considerably, we divided the non-adultlike responses into two categories: (1) looking responses (look briefly, watch continuously), and (2) moving responses (move, move to bolthole, move below ground). If the responses of young fell into the same category as the adult responses, i.e. either looking or moving, they were scored as similar; otherwise, they were scored as different. We analysed 323 responses from 48 young (26 females and 22 males, age range 19–180 days) in 19 litters and 10 groups.

**Playback Experiments**

**Recording methods and call selection**

We recorded alarm calls used for playback experiments at a distance of 1–2 m from the caller, and at 44.1-kHz sampling frequency, using a Sony digital audio tape recorder DAT-TCD D100 (frequency response: 20–20 000 Hz ±1 dB) connected to a Sennheiser directional microphone (K6 power module and ME66 recording head with a MZW66 pro windscreen; frequency response 40–20 000 Hz ±2.5 dB, Old Lyme, Connecticut, U.S.A.). Calls were uploaded on to a PC notebook and digitized (16-bits, 44.1 kHz) using the 24-bit U24 waveternal USB audio interface (Ego-sys, Seoul, Korea). Natural call sequences with a high signal-to-noise ratio were then prepared with Cool Edit 2000 (Syntrillium Software Corporation, Phoenix, Arizona, U.S.A.), and recorded back on to a DAT tape for use in the field.

Behavioural responses to alarm calls vary with predator type and urgency level, so we used six alarm call types: aerial and terrestrial calls at medium and high urgency levels and recruitment calls (elicited in response to snakes, birds such as faecal, urine or hair samples of other levels and recruitment calls (elicited in response to snakes, birds such as faecal, urine or hair samples of other snake species). These calls were played and until normal foraging behaviour was resumed after the call. The loudspeaker was hidden behind vegetation 5–10 m from the pup, and calls were played when the pup was at least 5 m from a bolthole or burrow system (after the first 2 weeks of emergence), at least 1 m from other individual and not engaged in vigilant behaviour. Calls were played only if there had not been a natural predator encounter during the preceding 20 min. To avoid habituation, the number of playback experiments was kept below the natural rate of alarm calling, and at least 3 days passed between successive playbacks in each group. A maximum of two playback experiments were conducted each day, with at least 1 h in between.

**Experimental protocol**

Responses to alarm calls without the presence of a predator were investigated by playing back calls to 11 groups. We conducted playbacks from first emergence ($\bar{X} \pm SD = 17 \pm 2.4$ days) until young reached an age of 95 days. We tested 16 randomly chosen individuals (eight females, eight males in 13 litters and nine groups) repeatedly over their development (typically every 2 weeks). These individuals received, on average, five playbacks each (range 2–7). The low numbers of playbacks for some individuals were due to bad weather conditions, depredation or technical difficulties. Other individuals, randomly selected for each playback, were tested only once. Overall, we tested 25 females and 16 males belonging to 23 litters in 146 playbacks (including 23 control playbacks). We conducted 14 alarm-call playbacks (aerial and terrestrial medium urgency and recruitment high urgency) and six control playbacks on eight litters in seven groups during the first 2 weeks of emergence (age range 24–30 days), when young stayed behind at the sleeping burrow together with one or several babysitters. All but one litter received multiple playbacks but with different call types. During these first 2 weeks, all pups in a litter typically stayed close together and showed the same response, so we obtained one response per litter. The remaining playbacks were conducted once young started foraging with the group ($\bar{X} \pm SD = 28 \pm 2.6$ days). Seven of the litters tested during the first 2 weeks of emergence were also tested again after foraging with the group.

Calls were played back with a Sony DAT-TCD D100 recorder connected to a Sony SRS-A60 loudspeaker (frequency response 70–20 000 Hz) and broadcast at amplitudes of 54–62 dB, measured 1 m in front of the speaker (Voltcraft 329 Sound Level Meter, Conrad Electronic, Hirschau, Germany; accuracy ±2 dB at 94 dB). This range of amplitudes corresponds to that observed for calls given during naturally occurring predator encounters. The duration of each playback was 3–20 s, depending on call type.

The focal pup was filmed with a Sony digital video camera DCR-PC 120E for at least 20 s before the call was played and until normal foraging behaviour was resumed after the call. The loudspeaker was hidden behind vegetation 5–10 m from the pup, and calls were played when the pup was at least 5 m from a bolthole or burrow system (after the first 2 weeks of emergence), at least 1 m from another individual and not engaged in vigilant behaviour. Calls were played only if there had not been a natural predator encounter during the preceding 20 min. To avoid habituation, the number of playback experiments was kept below the natural rate of alarm calling, and at least 3 days passed between successive playbacks in each group. A maximum of two playback experiments were conducted each day, with at least 1 h in between.

**Scan Sampling: Proximity to Adults**

To investigate how the spatial relationship between young and adults changed during development, we
collected data on 30 female young and 28 male young in 15 litters and 11 groups during three periods, using a scan-sampling procedure (Martin & Bateson 1993). The first period included the first 3 weeks of young foraging with the group (age range 33–54 days; N = 12 females, 8 males), the second period included week 6–8 (age range 70–93 days; N = 9 females, 13 males) and the third period week 11–13 (age range 106–125 days; N = 9 females, 7 males). Each individual was used as a subject only once. We collected scans on each individual during one morning foraging session, and every 15 min we recorded the distance to the nearest adult (<0.5 m: accuracy 0.1 m, >0.5 m: accuracy 0.5 m) on a Visor Pro handheld computer. On average, we obtained five scans per individual (range 2–6).

Data Analyses

Video analysis

Responses to playback experiments were quantified from videotapes using frame-by-frame analysis (12.5 frames/s) in Microsoft Windows Movie Maker version 5.1. We obtained the following measurements for both young and adults: (1) first response (see above), (2) most extreme response (see above), (3) latency to respond (time between onset of call and first response, hereafter referred to as reaction time), (4) response duration (time between onset and end of response, which was defined as the time when normal foraging behaviour was resumed and the individual did not return to vigilant behaviour within 30 s), (5) time spent scanning the surroundings (‘scanning time’) after the most extreme response, if this response involved movement (scanning time for looking responses was included in response duration), (6) the distance (≤2 m or >2 m) to nearest adult and (7) number of individuals within 1 m after the most extreme response.

Reaction time, response duration and scanning time were extracted only from playbacks conducted after young started foraging with the group. The responses of young and adults may not be independent, so we included in the analyses only those playbacks in which we could obtain measurements for both young and adults. Consequently, because we had incomplete data on adult measurements, sample size for each variable was reduced. Measurements on reaction time were extracted from 53 playbacks in 10 groups, response duration from 45 playbacks in 11 groups and scanning time from 30 playbacks in 10 groups.

Statistical analyses

All analyses were conducted using R for Microsoft Windows version 2.0.1 (R Development Core Team 2004) and the software packages nlme (http://www.r-project.org) and MASS (Venables & Ripley 2002). Where the assumptions of residual normality and variance homoscedasticity were violated, we transformed continuous variables with a natural logarithm. All tests were two tailed and based on type I sum of squares, thus controlling for preceding terms in the model. We first calculated the initial model including all explanatory variables and appropriate interaction terms. Significance level was set at \( P < 0.05 \), and factors with a \( P \) value above 0.10 were sequentially dropped. We identified the best model by comparing them using Akaike's information criterion (Pinheiro & Bates 2000). Predator type and urgency level were also included as potential explanatory variables, but these results are not presented here (L.I. Hollén & M.B. Manser, unpublished data).

We separately analysed behavioural observations, playback experiments and scans. Owing to the sampling procedure of some variables and incomplete measurements, our data were not fully balanced and sample size varies with analyses.

Behavioural observations. Unless otherwise stated, factors influencing the responses of young were analysed with a mixed-effects logistic regression model procedure characterized by a binomial error structure and logit link function. Mixed models allow both fixed and random effects to be incorporated (Pinheiro & Bates 2000; Venables & Ripley 2002). The models were fitted with penalized quasi likelihood estimation (PQL, glmmPQL function), which is a log likelihood estimation method for generalized models implemented in R (Breslow & Clayton 1993; Venables & Ripley 2002). We controlled for repeated sampling on young within different litters and groups by fitting individual identity nested within litter and group identity as a random term. Age, sex and helper-to-pup ratio were fitted as fixed effects. Individuals over 3 months old are more or less independent, so we calculated helper-to-pup ratios as the number of group members over 3 months old to the number under 3 months old. We compared the responses of young and adults by using chi-square tests.

Playback experiments. To investigate factors influencing the reaction time, response duration and scanning time of young, we used a linear mixed-effects model procedure fitted with residual maximum likelihood estimation (REML, lme function; Venables & Ripley 2002). Group identity was fitted as a random term and age, sex, helper-to-pup ratio, the number of individuals within 1 m after the most extreme response, and adult time as fixed effects. Unless otherwise stated, we also used a linear mixed-effects model procedure to compare the responses of young and adults. Playback situation nested within group identity was then fitted as a random term. This way, we controlled for repeated sampling within groups and dependencies between young and adults within each playback. Age class (young or adult) was fitted as a fixed effect. To investigate whether the proximity to adults influenced the likelihood of young looking towards others, we used a mixed-effects logistic regression model procedure with group identity fitted as a random term and age and distance to adults as fixed effects.

Scans. We used a linear mixed-effects model procedure (REML) with litter identity fitted as a random term and group identity was then fitted as a random term. This way, we controlled for repeated sampling on young within different litters and group identity as a random term. Age, sex and helper-to-pup ratio were fitted as fixed effects. Individuals over 3 months old are more or less independent, so we calculated helper-to-pup ratios as the number of group members over 3 months old to the number under 3 months old. We compared the responses of young and adults by using chi-square tests.
each individual were pooled and the mean distance to adults was used in the analysis.

RESULTS

Responses to Naturally Occurring Alarm Calls

Behavioural observations showed that young and adults did not differ in the likelihood of responding (responses listed in Table 1) to alarm calls (young: 89.4%; adults: 90.2%; Yates’ corrected chi-square test: \( \chi^2 = 0.02, P = 0.87 \)). However, in contrast to adults, young often responded to alarm calls uttered in response to non-dangerous birds (positive response, young: 88%; adults: 22%; \( \chi^2 = 18.76, P < 0.001 \)) but ignored those given in response to aerial predators far away (negative response, young: 48%; adults: 9%; \( \chi^2 = 7.16, P = 0.007 \)). However, the lack of response to aerial alarm calls never seemed to involve a great risk, because adults looked up only briefly in response to the same calls.

Young foraging with the group, especially before an age of 90 days, commonly ran to the nearest individual (42%, \( N = 159 \)) but looked less often towards other individuals (19%, \( N = 139 \)) when hearing an alarm call. The probability of responding independently of others increased with the age of young (running: \( F_{1,124} = 11.73, P = 0.0008; \) scan: \( F_{1,105} = 4.78, P = 0.03; \) Fig. 1a), but was not influenced by sex or helper-to-pup ratio (range of \( P \) values 0.26—0.65).

Although a large proportion (67%, \( N = 235 \)) of the independent responses were already adultlike, 82% (\( N = 33 \)) of the non-adultlike responses (not responding excluded) differed considerably from those of adults (significantly different from the hypothesized value of 50%, binomial test: \( P < 0.001 \)). Young often moved to shelter when adults looked up only briefly (19/27 cases) or looked up briefly when adults moved (8/27). The probability of showing adultlike responses increased as young grew older (\( F_{1,192} = 12.07, P = 0.0006; \) Fig. 1b), and 87% of the non-adultlike responses were shown before an age of 90 days. Independent of age (sex*age: \( F_{1,193} = 0.43, P = 0.51 \)), female young were more likely to show adultlike responses than were male young (\( F_{1,197} = 5.21, P = 0.02; \) Fig. 1b). Helper-to-pup ratio did not influence the probability of showing adultlike responses (\( F_{1,196} = 0.31, P = 0.58 \)), but looking towards other individuals as a first response influenced the subsequent behaviour of young. Although only 23 of 119 most extreme responses were non-adultlike, 74% of them were shown by young responding independently instead of looking towards other individuals (binomial test: \( P = 0.04 \)).

Responses to Playback Experiments

The results of the playback experiments corroborated observational data in suggesting that young and adults are equally likely to respond to alarm calls. Both young and adults responded to all alarm call playbacks (\( N = 123 \)) but to none of the control (birdsong) playbacks (\( N = 23 \)). However, during the first 2 weeks of emergence, when playbacks were conducted on young and adults (\( N_Y = N_A = 14 \)) staying behind at the sleeping burrow, all alarm calls caused the majority of young (79%) to move either below ground or closer to the entrance. In contrast, the majority of adults (79%) looked up only briefly in response to the same alarm calls (Yates’ corrected chi-square test: \( \chi^2 = 7.00, P = 0.008 \)).

When foraging with the group, young commonly ran to the nearest individual but seldom looked towards others (running: 50%; looking: 23%, \( N = 120 \)), supporting the results of observational data. Young staying further away from adults were more likely to look towards others before responding than were young staying in close proximity (\( F_{1,62} = 7.12, P = 0.01 \)). Again, most (82%, \( N = 38 \)) of the independent responses were already adultlike.

Despite a strong influence of adult reaction time (\( F_{1,36} = 34.79, P < 0.001 \)), young reacted more slowly than did adults (\( F_{1,32} = 6.17, P = 0.02 \); Fig. 2a). Female young tended to react faster than did male young (\( F_{1,36} = 2.95, P = 0.09 \)). However, when the paired adult reaction times were controlled for, this difference disappeared (\( F_{1,36} = 1.74, P = 0.19 \)). Compared to adults, young also resumed foraging faster (\( F_{1,44} = 17.97, P < 0.001; \)
Fig. 2b) and spent less time scanning the surroundings ($F_{1,29} = 17.9, P < 0.001$; Fig. 2c). Female young resumed foraging more quickly than did male young (duration: $F_{1,30} = 5.52, P = 0.03$). Response duration was not influenced by adult response duration ($F_{1,27} = 1.14, P = 0.30$), or the number of individuals within 1 m after the most extreme response ($F_{1,30} = 2.09, P = 0.16$). In contrast, young increased the time spent scanning with increasing adult scanning time ($F_{1,16} = 11.00, P = 0.004$), and tended to scan longer with fewer individuals around ($F_{1,16} = 3.69, P = 0.07$). Again, when the paired adult scanning times were controlled, this tendency disappeared ($F_{1,16} = 2.17, P = 0.16$). Reaction time, response duration and scanning time did not change during the first 3 months of age and were not influenced by helper-to-pup ratio (range of $P$ values: 0.30–0.83).

Proximity to Adults

The distance between young and adults increased with the age of young ($F_{1,13} = 15.07, P = 0.002$; Fig. 3). Independent of age (age*sex: $F_{1,41} = 0.78, P = 0.38$), female young stayed closer to adults than did male young ($F_{1,41} = 5.65, P = 0.02$; Fig. 3). Helper-to-pup ratio did not influence the distance between young and adults ($F_{1,12} = 0.22, P = 0.64$).

DISCUSSION

Although young meerkats were as likely as adults to respond to alarm calls, responses differed from those of adults in a number of ways. Unlike adults, young often responded to nondangerous stimuli and ran for shelter when not necessary. Young also reacted more slowly and resumed foraging earlier than did adults after playbacks of alarm calls. However, as young grew older, their responses also became increasingly adultlike. Behavioural observations showed that the greatest change towards adultlike behaviour occurred before reaching independence at 3 months of age. For unknown reasons, changes in reaction time, response duration and scanning time seem to occur later. Although these results may indicate that experience is needed to adjust the responses of young, correct responses were shown early in development. One probable explanation is that, despite giving parental care, thus providing the opportunity for the pups to learn how to avoid predators, adult meerkats engage in little active defence. Thus, young meerkats may be under equally high pressure as young in species without parental care to acquire correct alarm call responses rapidly (e.g. Miller & Blaich 1986; Göth 2001), especially because predation is the major source of pup mortality (Clutton-Brock et al. 1999b).

Despite abundant evidence that animals are capable of improving their responses as a result of experience (reviewed in Griffin et al. 2000), these developmental changes could be the result of maturation rather than experience. However, the development of antipredator behaviour is likely to be a complex process that relies on an interaction between maturational processes and learning, so it may be inappropriate to discard the role of either...
one of these processes. For example, newly emerged pups ignored playbacks of birdsong but behaved as though they did not discriminate between different alarm calls and entered a burrow in response to almost all playbacks. Furthermore, young foraging with the group often moved to shelter when adults only looked up briefly. These results might suggest that young are predisposed to recognize features of alarm calls from other irrelevant sounds, but with time they learn to discriminate between the different alarm calls and associate them with the threat that they pose (see also Davies et al. 2004). However, a simple maturation of the discrimination threshold could also explain these results. The optimal threshold will depend on the costs of treating a nonthreatening signal as an alarm or ignoring a true alarm (Reeve 1989; Sherman & Leger 1997). The cost of running below ground during the first few weeks of emergence is unlikely to be high because pups remain near their sleeping burrow, but doing so may increase survival because young escape visual detection by the predator. Depending on the type of predator, foraging young may also be safer if they are already at shelter when predators approach. Therefore, lower thresholds for moving could be selected in young because of their high predation risk.

Our playback experiments also showed that young resumed foraging earlier and spent less time scanning the surroundings than did adults. Many studies have shown that juvenile mammals are commonly less vigilant than adults despite their greater risk of predation (e.g. Arenz & Leger 2000). A higher nutritional demand in juveniles (e.g. Arenz & Leger 2000), and thus strong selection on intense foraging, may lead young to rely on the vigilance of other individuals (Loughry & McDonough 1989). In meerkats, factors affecting daily weight gain are likely to be under strong selection because daily weight gain is positively related to survival throughout the first year of life (Clutton-Brock et al. 2001). The differences found between young and adults may therefore simply reflect differences in nutritional requirements, but they could also be because young are unable to assess the risk associated with the alarm calls.

In addition to associative learning, other learning mechanisms such as simple habituation and/or observational learning (Moore 2004) may be responsible for some of the observed changes in pup behaviour. First, a selective habituation process, where responses to frequent nonpredator stimuli diminish and responses to infrequent predator stimuli are maintained, could underlie the lack of responses to alarm calls given by adults in response to birds. Second, although young do not simply copy the behaviour of adults, they occasionally seem to make use of social information provided indirectly from the responses of other group members. Both the time to react and the time allocated to vigilance after playbacks were strongly influenced by adult behaviour. In addition, even though the number of adults present did not influence the behaviour of young, very young individuals in particular often ran to the nearest individual. This response is similar to that of infant vervet and squirrel monkeys, Saimiri sciureus, which commonly run to their mothers when alarmed (Seyfarth & Cheney 1986; McCowan et al. 2001). Looking towards other individuals was less common, but also similar to responses of vervet monkeys (Seyfarth & Cheney 1986); young doing so were more likely to show adultlike responses than young that responded independently.

Young could, however, gather helpful cues from other individuals without intentionally seeking them. First, the result that young reacted more slowly than adults after playback of an alarm call suggests that young may wait for adults to react before reacting themselves. Second, young staying further away from adults were more likely to look towards others than were young staying closer. Finally, female young, which remained in closer contact to other group members than did male young, tended to react faster and were also more likely to show adultlike responses. This result does not necessarily mean that females are generally better at responding, especially because the reaction time was strongly influenced by adult time, but young females may be more likely to gather cues from others. However, the difference in distance to adults between male and female young was fairly small, so whether this has implications for the ability to show adultlike responses remains to be thoroughly investigated.

Our results may also be compatible with a different perspective, formulated for both mammals (Owings & Loughry 1985; Hersek & Owings 1994; Hoffman et al. 1999; Hanson & Coss 2001) and birds (Platzen & Magrath 2005), suggesting that, instead of viewing the responses of young as imperfect versions of adult responses, young should be seen as adopting an optimal response for their developmental stage. The idea seems to be widely applicable, and it would not be surprising that selection may favour responses that increase juvenile survival at their current stage in development, given their high vulnerability. However, whether the behaviour of meerkat young represents age-adaptive changes or not remains an open question, because
our results seem equally consistent with the idea of young showing imperfect versions of adult behaviour.

Although we cannot rule out the possibility that young could be responding directly to predators or nondangerous birds rather than to any call uttered by other group members during natural observations, this conclusion seems unlikely where predators are concerned. First, young individuals mostly showed a response before detecting the predator themselves. Second, the results of our playback experiments, in which the presence of a predator was controlled for, corroborated those of natural observations. However, even with playback experiments, we cannot discount that young may occasionally respond to cues from other group members rather than the alarm calls themselves.

To conclude, we suggest that the observed differences in alarm call responses between young and adult meerkats could be caused by several mechanisms (and their interactions), including maturation, nonassociative learning and associative learning. Furthermore, although young may have the capacity to acquire appropriate alarm call responses independently, our results indicate that they may gain from using cues available from other group members. Perhaps as a result of spending less time in close interactions, young may occasionally respond to cues from other group members rather than the alarm calls themselves.

Acknowledgments

We are indebted to Tim Clutton-Brock for scientific advice and for allowing us to work on the meerkat population of the Kalahari Meerkat Project. We are also grateful to Mr and Mrs Hennie Kotze for the permission to work on their land, to Johan Du Toit and Martin Haupt at the Mammal Research Institute, University of Pretoria, for logistical support, and to all students and volunteers contributing help throughout this study. Thanks to Hansjoerg Kunc, Alan McElligott and three anonymous referees for helpful comments on the manuscript. This project was funded by a grant given to M.B.M. from the Swiss National Science Foundations, SNF-Förderprofessur No. 631-066129.

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