

The development of foraging microhabitat preferences in meerkats

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Animals of many species tend to target their foraging attempts toward particular microhabitats within their habitat. Although these preferences are critical determinants of the foraging niche and have important ecological and evolutionary implications, we know little about how they develop. Here, we use detailed longitudinal data from meerkats (*Suricata suricatta*) to examine how individual learning and the use of social information affect the development of foraging microhabitat preferences. Despite living in an open, arid environment, adult meerkats frequently foraged at the base of vegetation. Young pups seldom did so, but their foraging microhabitat choices became increasingly adult-like as they grew older. Learning about profitable microhabitats may have been promoted in part by positive reinforcement from prey capture. Foraging may also have become increasingly targeted toward suitable locations as pups grew older because they spent more time searching before embarking on foraging bouts. The development of microhabitat preferences might also have been influenced by social cues. Foraging in close proximity to adults may increase the probability that pups would dig in similar microhabitats. Also, pups often dug in holes created by older individuals, whereas adults never dug in existing holes. Foraging in existing holes was no more profitable to pups than creating their own foraging hole but could provide pups with important informational benefits. The integration of personal and social information is likely to be a common feature in the development of the foraging niche in generalist species. *Key words*: development, foraging, learning, meerkats, social information, *Suricata suricatta*. [*Behav Ecol* 20:103–110 (2009)]

INTRODUCTION

Animals commonly target their foraging attempts toward specific microhabitats within their habitat (Lack 1971; Bernays and Chapman 1994; Grant BR and Grant PR 2003). Such microhabitat foraging preferences are critical in determining the niche occupied by individuals and as such may have important effects on spatial segregation, the coexistence of closely related species, and speciation (Lack 1971; Grant BR and Grant PR 2003; Beltman et al. 2004). However, relatively little is known about the processes underlying the development of individuals' preferences for particular microhabitats in which to search for food.

Although the foraging niche may be largely constrained by morphological features, there is increasing evidence that many aspects of foraging behavior are honed and modified through life (Krebs and Inman 1992; Dall and Cuthill 1997). Adult animals' microhabitat foraging preferences may often result in large part from individual experiences in early life (Immelmann 1975; Galef and Giraldeau 2001; Davis and Stamps 2004). For example, in certain insect species, individuals feed exclusively on the plant species on which they were born (Bernays and Chapman 1994). In other animals, individuals may learn through trial and error that certain microhabitats are more likely to yield prey than others, consequently targeting their foraging attempts toward more profitable areas (Giraldeau 1984).

In species where young remain dependent on adults for extended periods, such individual learning is likely to be complemented by information acquired through social experiences (King 1994; Galef and Giraldeau 2001; Danchin et al. 2004).

Such social experiences are likely to be particularly important in the development of foraging behavior of generalist species, where young must learn to select a wide range of different food types (Klopfer 1961; Lefebvre 2000) and in species such as carnivores (Bekoff et al. 1984; Kitchener 1999; Nel 1999) and extractive foragers (Parker and Gibson 1977; Gunst et al. 2008), where food acquisition involves considerable skill. In such species, interactions with older, more experienced conspecifics commonly have major effects on the development of components of foraging behavior including the location of foraging patches (Giraldeau 1984; King 1994), food preferences (Galef 2003; Visalberghi and Addessi 2003; Addessi et al. 2005; Thornton, 2008b), and food-handling skills (Caro 1980; Aisner and Terkel 1992; Thornton and McAuliffe 2006). However, although there is considerable evidence that the presence of conspecifics and the cues they leave behind can promote learning of the location of specific foraging sites and routes in the short term (Galef and Giraldeau 2001; Reader et al. 2003), it is less clear whether social influences can lead to more general, long-term changes in foraging microhabitat choices.

Recent cross-fostering experiments between blue tits, *Cyanistes caeruleus*, and great tits, *Parus major*, demonstrated that individuals shifted their ecological niche toward that of their foster species (Slagsvold and Wiebe 2007), providing support for the idea that early social experiences can play a critical role in determining life-long foraging microhabitat preferences. However, further work is necessary to determine the social cues that young animals attend to and how such social information combines with individual learning to affect the development of microhabitat foraging preferences. Detailed data on changes in microhabitat choices with age, the rewards obtained from foraging in different microhabitats and cues obtained through foraging with others are therefore critical if we are to further our understanding of how animals come to occupy their foraging niches.

Here, we use longitudinal data to investigate how individual experience and the use of social information may influence the

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development of meerkats' microhabitat preferences. Meerkats are cooperatively breeding mongooses living in groups of 2–50 individuals in semi-arid regions of southern Africa. Groups comprise a dominant male and female, who monopolize breeding, and a variable number of helpers of both sexes that assist in feeding pups (Brotherton et al. 2001; Clutton-Brock et al. 2001). Pups begin foraging with their social group at around 30 days of age and are provisioned by all group members in response to begging calls (Doolan and Macdonald 1996; Manser and Avey 2000). Pups learn what to eat through social learning from more experienced group members (Thornton, 2008b) and are taught to kill and disable difficult prey (Thornton and McAuliffe 2006). Although it is not yet known how pups learn where to look for food, it is clear that their efficiency at digging for buried items (Thornton 2008a) and handling prey (Thornton and McAuliffe 2006) improves with age until they reach nutritional independence at around 90 days of age.

Meerkats are a generalist species, feeding on a wide range of invertebrate and small vertebrate prey, which they find by digging in sand. Although they forage in open terrain with sparse vegetation cover, adult meerkats commonly target their foraging attempts at the base of vegetation (Thornton A, personal observation). In this study, we use detailed data from foraging focal watches to investigate how preferences for foraging in this microhabitat develop. First, we examine how pups' microhabitat choices (i.e., foraging in the open or at the base of vegetation) change with age, compare the microhabitat choices of pups to those of adults in their group, and investigate the foraging returns gained from different microhabitats. We then examine whether pups learn to give up unproductive bouts by analysing the time pups spend searching before embarking on a foraging bout and how the duration of individual bouts varies with pup age. Finally, as pups generally forage in close proximity to adults and commonly dig in foraging holes created by older individuals, we investigate the possible nutritional benefits pups might gain from digging in holes created by their elders and discuss whether this behavior may generate cues that help to promote learning of the profitability of different microhabitats.

METHODS

Data were collected from March 2005 to April 2006 from meerkats living in 11 groups of 6–41 individuals in semi-desert along the dry Kuruman River, 27 km west of Van Zylsrus in the South African Kalahari (26°58'S, 21°49'E). Habitat at the study site consists of sand dunes and flat terraces adjoining the riverbed, sparsely vegetated with low shrubs (*Grewia* spp. and *Rhigozum trichotomum*), perennial grasses including *Aristida* spp., *Eragrostis* spp., and *Stipagrostis* spp., and occasional *Acacia* and *Boscia* trees. Full details of habitat and climate have been published previously (Russell et al. 2002). Groups were located by radio tracking-collared animals, and all individuals were identifiable from unique dye marks on their fur. All animals were habituated to close observation (<1 m) and more than 90% could be weighed regularly by enticing them onto an electronic top-pan balance using crumbs of hard-boiled egg. The residuals of a regression of morning weights (preforaging) in grams against age in days were used to obtain a measure of how heavy an individual was for its age on a particular day (hereafter "age-corrected weight").

To investigate patterns of foraging, we conducted 319 focal watches on 58 pups (individuals < 90 days) from 22 litters in 10 groups (mean = 5.5 ± 0.6 focal watches per pup, range = 1–15) and 271 focal watches on 105 helpers from 50 litters in 11 groups (mean = 2.6 ± 0.2 focal watches per helper, range = 1–9). Helpers are defined as all individuals more than

3 months old, which can potentially contribute to feeding pups (Brotherton et al. 2001). Unless otherwise stated, all multifactorial analyses presented use these data sets. During each focal watch, we noted the duration and microhabitat type of every foraging bout and the time spent searching in between foraging bouts. "Searching" was defined as an individual walking with its head oriented toward the substrate, sniffing regularly but not digging. This behavior is used to locate suitable foraging sites before beginning to dig (Barnard 2000). A "foraging bout" was defined as a period during which the individual scratched or dug in sand in an attempt to find food. Bouts were classed as being at the base of vegetation if the focal animal foraged under the canopy cover of trees, shrubs, or dense clumps of grass. Other foraging bouts were classed as being located in the open. We also noted whether a foraging bout was in a location initiated by the focal animal or in a hole previously dug by another individual. Holes dug by other individuals were clearly identifiable through piles of recently displaced sand accumulated around the hole. On the majority of occasions (626/670 bouts = 93.4%), we were able to record the identity of the individual that originally dug the hole. Focal watches lasted 20 min, but if the focal individual was engaged in an activity (e.g., digging) at the end of the 20-min period, the focal watch was not ended until the individual changed activities (mean focal watch duration = 1208 ± 10 s). Focal watches were paused if the group ceased foraging for more than 30 s, for example, because they had detected a predator. Data were recorded on a Zire 21 handheld computer (Palm, Sunnyvale, CA), and times were accurate to 1 s.

For each foraging bout, we recorded whether the bout resulted in prey capture. For successful bouts, we noted the type (e.g., gecko, scorpion) and size of all items found. Prey items were divided into 5 size categories: tiny (items swallowed immediately), small (items fitting entirely in an adult's mouth), medium (less than half the item protruding from an adult's mouth), large (more than half the item protruding), and extra-large (more than 80% of the item protruding), as per Thornton (2008a). Mean wet mass values for each category were tiny = 0.05 g, small = 0.11 g, medium = 0.58 g, large = 2.86 g, and extra-large = 9.56 g (Scantlebury M, unpublished data). Tiny prey items included ants, ant larvae, termites, and termite larvae and accounted for about 5% of total prey biomass (Thornton A, unpublished data). These items typically occurred in small patches (e.g., ants and ant larvae at a nest) and were divisible (i.e., more than one meerkat could potentially share the food resource). All other prey items occurred singly and were indivisible.

Statistical analyses

All data were analyzed in Genstat 8.1 (Rothamstead Experimental Station, Harpenden, UK). Multifactorial analyses were conducted using linear mixed models (LMM) or generalized linear mixed models (GLMM) for normal and nonnormal error structures, respectively. Mixed models are similar to general linear models but allow both fixed and random effects to be fitted, with random terms controlling for repeated measures such as group, litter, and individual identities (Schall 1991). Models were implemented with a nested structure such that individual identities were nested in litters and litters were nested in groups. As multiple focal watches conducted at a group on a given day were within the same territory area, they were assigned a unique territory identity, which was also included as a random factor. Initially, all likely explanatory variables were entered into the model. All possible 2-way interactions between them were investigated, and terms were sequentially dropped until the minimal model contained only terms whose elimination would significantly reduce the

explanatory power of the model. Wald statistics and probability values for significant terms were derived from having all significant terms in the model, whereas values for nonsignificant terms were obtained by adding each term individually to the minimal model. For all multifactorial analyses, we fitted age (in days) and age-corrected weight as core explanatory variables. All models also included sex; rainfall (measured as the total rainfall, in mm, during the 30 days prior to the day of the focal watch), which is known to affect food availability (Doolan and Macdonald 1996); time of day (morning or afternoon), as foraging behavior varies over the course of the day; and litter size and helper number (number of group members > 3 months old) on the day of the focal watch, as these may influence the availability of social cues to individual pups. Following Pinheiro and Bates (2000), all random terms were initially included in models, and nonsignificant random terms were sequentially dropped. To verify the robustness of the results, we also ran all models retaining nonsignificant random terms. This made no qualitative difference to the results of the models presented.

Microhabitat choices and success

To investigate whether pups' microhabitat choices changed with age, we conducted a GLMM on the proportion of bouts in a focal watch that were at the base of vegetation. Data were fitted to a binomial distribution with logit-link function with the number of foraging bouts at the base of vegetation fitted as the numerator and the total number of bouts (not including bouts conducted in holes dug by others) fitted as the denominator. We also investigated whether the microhabitat choices of pups became more similar to those of adults in their group as the pups aged using paired analyses. Pups were divided into 2 age categories: young (<55 days) and old (>65 days). Focal watches were conducted on 8 pups from 5 litters in 4 groups. To compare pup and adult behavior, we also conducted focal watches on adult helpers (>1 year) in the group on the same day and foraging session (morning or evening) as the pup focal watches. For each focal watch on each pup, we calculated the proportion of foraging bouts initiated by pups (i.e., excluding bouts where the pup foraged in a hole dug by another individual) that were at the base of vegetation. We then calculated the average proportion of bouts at the base of vegetation for all focal watches on adults conducted in the same foraging session on the same day (1–4 adults per pup per day, mean = 2.1 ± 0.1). We averaged these values for each pup for both age categories (1–5 focal watches per pup per category, mean = 2.3 ± 0.3) and used paired *t*-tests to compare the similarity of foraging locations of adults and pups in their group when the pups were young and old. An analysis of variance (ANOVA), blocking for pup–adult pair and with category (pup or helper) and pup age (<55 days or >65 days) fitted as explanatory variables, was used to verify that changes in pup behavior, rather than variation in the behavior of adults in the 2 tests were responsible for observed differences.

Pups' microhabitat choices may be influenced in part by foraging returns gained in different microhabitats. To investigate whether pups foraging at the base of vegetation differed in their success rates from pups foraging in the open, we used a GLMM with a binomial response (1 or 0) indicating whether or not the bout was successful. In addition to the core variables, we included bout duration (in seconds, log transformed) and whether or not the bout was in a hole created by another individual as potential explanatory terms. To control for repeated measures within focal watches, each focal watch was assigned a unique identity and focal identity was included as an additional random factor. Finally, to investigate whether foraging at the base of vegetation or in the open yielded prey of

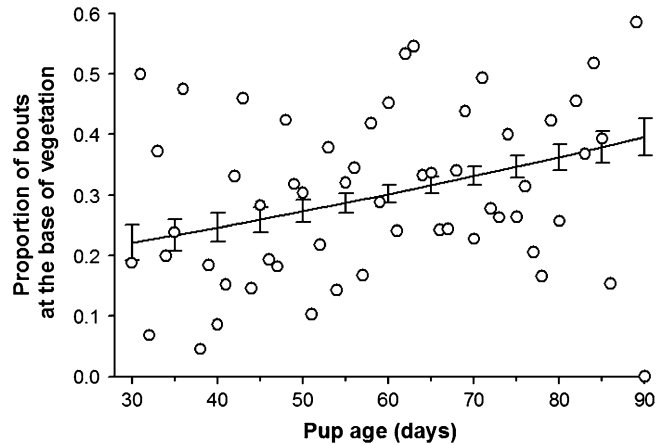


Figure 1

The proportion of bouts pups conducted at the base of vegetation increased with age ($P = 0.011$). Dots are means from raw data; line is predicted means from a GLMM \pm standard error.

different mass, we conducted paired analyses on the average mass of food found by individuals in each of the 2 locations during focal watches. As young pups rarely found prey, we used only pups more than 65 days old for analysis of pup foraging success. The analysis used only focal watches in which pups found at least one prey item in each of the 2 locations (open and base of vegetation). Prey-mass values were averaged per pup, and a paired *t*-test was conducted using 25 pups from 13 litters in 8 groups (1–5 focal watches per pup, mean = 2 ± 0.2). We also conducted a similar analysis for helpers, using data from 52 adult helpers from 11 groups (1–6 focal watches per helper, mean = 2 ± 0.2).

Searching and bout durations

Spending time searching for suitable locations before embarking on a foraging bout may allow individuals to identify locations likely to yield prey. To investigate whether pups invested more time in searching before embarking on a foraging bout as they aged, we conducted a LMM analysis on the average duration of individual bouts of searching during a focal watch. Average search bout duration (in seconds) was normalized for analysis using a log transformation. The analysis used data from 319 focal watches on 58 pups from 22 litters in 10 groups (mean = 5.5 ± 0.6 focal watches per pup, range = 1–15).

Pups may learn to give up unproductive bouts through experience. We examined factors affecting the duration of individual foraging bouts (both successful and unsuccessful) using a LMM with the response term (in seconds) log transformed. The analysis was conducted on 8047 foraging bouts from 319 focal watches on 58 pups from 22 litters in 10 groups (mean = 5.5 ± 0.6 focal watches per pup, range = 1–15). Both successful and unsuccessful bouts were included, and focal identity was included as an additional random term. In addition to the core explanatory variables, we also included whether the bout was at the base of vegetation. We then conducted a separate LMM analysis to investigate whether the duration of unsuccessful bouts changes with pup age, using only the 7324 unsuccessful foraging bouts from the 319 focal watches.

Social cues

Digging in holes dug by other individuals could provide nutritional and/or informational benefits to pups. We examined the factors affecting the proportion of foraging bouts that pups

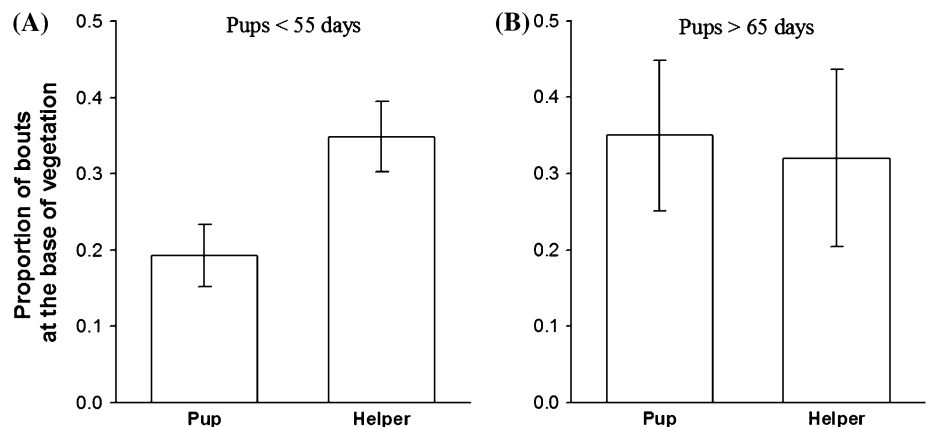
Table 1
GLMM on factors affecting the proportion of foraging bouts that pups foraged at the base of vegetation

Full model	Wald statistic (χ^2)	Degree of freedom	<i>P</i>
Pup age (days)	6.43	1	0.011
Helper number	4.96	1	0.026
Time of day (AM, PM)	3.96	1	0.047
Rainfall (mm)	2.04	1	0.154
Litter size	1.18	1	0.277
Pup age-corrected weight	0.76	1	0.385
Pup sex	0.30	1	0.548
Minimal model	Average effect	Standard error	
Constant	-0.84	0.088	
Pup age (days)	0.013	0.0054	
Helper number	0.029	0.011	
Time of day			
AM	0	0	
PM	0.34	0.17	

Data were fitted to a binomial distribution with logit-link function with the number of foraging bouts at the base of vegetation during a focal watch fitted as the numerator and the total number of bouts fitted as the denominator. Analysis used data from 319 focal watches on 58 pups from 22 litters in 10 groups (mean = 5.5 ± 0.6 focal watches per pup, range = 1–15). Territory and pup identities constituted significant repeatability ($P < 0.05$), but group, litter, and individual identities were not significant random factors.

conducted in holes dug by others using a GLMM. Data were fitted to a binomial distribution with a logit-link function, with the number of foraging bouts in holes dug by others during a focal watch fitted as the numerator and the total number of bouts fitted as the denominator. As helpers were likely to have removed prey items from foraging holes, we predicted that when pups did find prey in holes dug by others, the prey would be more likely to consist of tiny items such as ant larvae left behind by helpers. We tested this hypothesis using a GLMM on successful pup foraging bouts, with binary response terms (1 or 0) indicating whether or not the prey item was tiny. In addition to the core explanatory variables, we included whether or not the bout was in a hole dug by another. Focal identity was included as an additional random term. The analysis was conducted on 723 successful foraging bouts from 209 focal watches on 52 pups from 21 litters in 10 groups (mean = 4.0 ± 0.4 focal watches per pup, range = 1–10).

Figure 2
 (A) Pups younger than 55 days conducted a significantly lower proportion of foraging bouts at the base of vegetation than adult helpers in their group ($P = 0.015$). (B) Once they were more than 65 days old, there was no significant difference ($P = 0.377$). Category (pup or helper) and age (<55 days, >65 days) interacted significantly: ANOVA; $F_{1,32} = 7.16$, $P = 0.014$.



RESULTS

Microhabitat choices and success

On average, helpers conducted a substantially higher proportion of their foraging bouts at the base of vegetation than pups (helpers: mean = 0.29 ± 0.015 , pups: mean = 0.19 ± 0.0091). Pups were increasingly likely to forage at the base of vegetation as they grew older (Figure 1, Table 1) and when there were more helpers in the group (Table 1) and their microhabitat preferences became more similar to those of adults in their group as they aged. Pups younger than 55 days conducted a significantly lower proportion of foraging bouts at the base of vegetation than adult helpers in their group (paired *t*-test: $t_8 = 3.19$, $P = 0.015$; Figure 2A), but there was no significant difference once pups were older than 65 days ($t_8 = 0.94$, $P = 0.377$; Figure 2B; ANOVA interaction term: $F_{1,32} = 7.16$, $P = 0.014$).

Changes in microhabitat preferences may be partly explained by positive conditioning due to payoffs from foraging in different microhabitats. For pups younger than 55 days, only 91 out of 2570 (=3.5%) of foraging bouts resulted in prey capture, but the probability a bout would be successful increased with age and rainfall (Table 2). Controlling for these effects, bouts at the base of vegetation were more likely to be successful than bouts in the open, particularly if they were of long duration (Figure 3, Table 2). However, microhabitat did not appear to affect the size of prey items found by pups in successful bouts: paired analysis of the average mass of prey found by pups more than 65 days old at the base of vegetation or in the open showed no significant difference (paired *t*-test: $t_{25} = 0.39$, $P = 0.697$), and GLMM analysis revealed no effect of microhabitat on probability a successful bout would yield tiny prey (Table 3). In contrast, prey items found by adults at the base of vegetation had significantly higher average mass than items found in the open (base of vegetation: 0.73 ± 0.23 g, open: 0.29 ± 0.073 ; Wilcoxon matched-pairs test, $n = 49$, $T = 321$, $P = 0.003$).

Searching and bout durations

Young pups invested little time in searching before embarking on a foraging bout, but the average duration of individual bouts of searching increased with age (LMM: $\chi^2 = 34.18$, degree of freedom = 1, $P < 0.001$; no other explanatory terms were significant in the model [$P > 0.250$]). Pup foraging bouts at the base of vegetation were longer than those in the open, controlling for other significant terms (Table 4A). Although there was no significant effect of pup age on the

Table 2
GLMM on factors affecting the probability that a foraging bout would result in prey capture

Full model	Wald statistic (χ^2)	Degree of freedom	<i>P</i>
Log bout duration (s)	363.89	1	<0.001
Pup age (days)	83.52	1	<0.001
Rainfall (mm)	10.81	1	0.001
Log bout duration × bout location	8.93	1	0.003
Bout location (open, base of vegetation)	4.17	1	0.041
Helper number	3.30	1	0.069
Adult hole (yes, no)	1.41	1	0.235
Time of day (AM, PM)	1.30	1	0.254
Pup age-corrected weight	0.17	1	0.683
Litter size	0.13	1	0.721
Pup sex	0.06	1	0.806
Minimal model	Average effect	Standard error	
Constant	-2.13	0.089	
Log bout duration (s)	1.94	0.10	
Pup age (days)	0.045	0.0050	
Rainfall (mm)	0.0055	0.0017	
Log bout duration × bout location			
Open	0	0	
Base of vegetation	0.65	0.022	
Bout location			
Open	0	0	
Base of vegetation	0.19	0.095	

Data were fitted to a binomial distribution with a logit-link function and binary response terms (1 or 0) indicating whether or not the bout was successful. Analysis was conducted on 8047 foraging bouts from 319 focal watches on 58 pups from 22 litters in 10 groups (mean = 5.5 ± 0.6 focal watches per pup, range = 1–15). Territory and focal identities constituted significant repeatability (*P* < 0.05), but litter, individual, and group identities were not significant random factors.

duration of individual foraging bouts overall, analysis restricted to unsuccessful bouts showed that the duration of each foraging bout became shorter as pups aged, controlling for the effects of bout location and time of day (Table 4B).

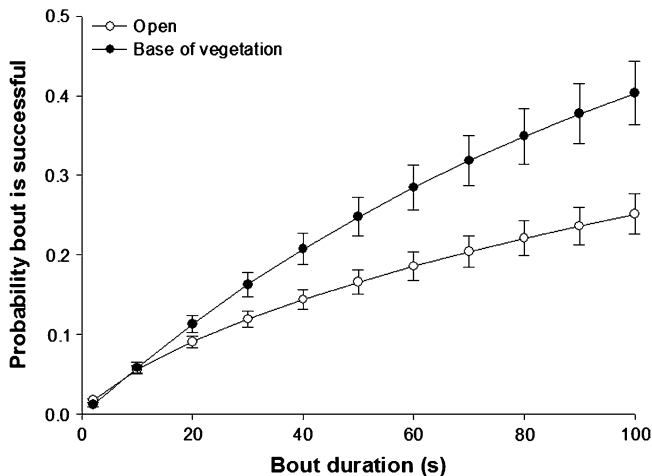


Figure 3
Effect of bout duration (s) and bout location on the probability that a foraging bout was successful (bout duration × location: *P* = 0.03).

Table 3
GLMM on factors affecting the probability that prey found in successful foraging bouts was tiny

Full model	Wald statistic (χ^2)	Degree of freedom	<i>P</i>
Log ₁₀ bout duration (s)	9.57	1	0.002
Time of day (AM, PM)	6.42	1	0.011
Hole dug by other (yes, no)	5.68	1	0.017
Pup age (days)	2.02	1	0.155
Pup age-corrected weight	0.81	1	0.368
Rainfall (mm)	0.35	1	0.554
Litter size	0.15	1	0.694
Bout location (open, base of vegetation)	0.16	1	0.694
Helper number	0.09	1	0.768
Pup sex	0.05	1	0.823
Minimal model	Average effect	Standard error	
Constant	-1.62	0.28	
Log ₁₀ bout duration (s)	-0.76	0.24	
Time of day			
AM	0	0	
PM	0.82	0.32	
Hole dug by other			
Yes	0	0	
No	-1.08	0.45	

Data were fitted to a binomial distribution with a logit-link function and binary response terms (1 or 0) indicating whether or not the prey item was tiny. Analysis was conducted on 723 successful foraging bouts from 209 focal watches on 52 pups from 21 litters in 10 groups (mean = 4.0 ± 0.4 focal watches per pup, range = 1–10). Territory, focal, and group identities constituted significant repeatability (*P* < 0.05), but litter and individual identities were not significant random factors.

Social cues

Pups frequently dug in holes previously made by other individuals (mean = 9.9% of all foraging bouts in a focal; Figure 4), whereas helpers were never seen to do so (*N* = 5420 foraging bouts). Foraging bouts conducted by pups in existing holes typically occurred in holes created by helpers, rather than other pups (622 out of the 626 foraging bouts in which the identity of the original digger was known = 99.4%). The proportion of foraging bouts conducted in holes created by others declined with pup age (Figure 4) and with increasing rainfall, and there was a negative effect of litter size (Table 5).

Digging in holes dug by others appeared to provide few immediate nutritional benefits to pups. Bouts conducted in such locations were no more likely to result in prey capture than bouts in locations initiated by pups (*P* = 0.235; Table 2), even though they tended to be of significantly longer duration (Table 4). Analysis of successful bouts showed that when pups did find prey in holes dug by others, the prey were more likely to be tiny items than when pups created their own foraging holes (Table 3).

DISCUSSION

Meerkats live in arid, open environments where vegetation is sparse and widely dispersed. Nevertheless, adults conducted almost a third of their foraging bouts at the base of vegetation, suggesting that they actively seek out this microhabitat to look for prey. The findings presented here suggest that meerkats' microhabitat preferences develop as a result of learning through experience in early life. The use of cues generated

Table 4
LMMS on factors affecting the duration of (A) all foraging bouts and (B) unsuccessful bouts only

Full model	Degree of freedom	(A) All bout durations		(B) Unsuccessful bout durations	
		Wald statistic (χ^2)	<i>P</i>	Wald statistic (χ^2)	<i>P</i>
Bout location (open, base of vegetation)	1	109.04	<0.001	91.36	<0.001
Hole dug by other (yes, no)	1	36.65	<0.001	33.84	<0.001
Time of day (AM, PM)	1	3.82	0.051	5.04	0.025
Pup age (days)	1	2.14	0.143	12.49	<0.001
Rainfall (mm)	1	2.02	0.155	0.52	0.469
Pup age-corrected weight	1	0.58	0.447	0.52	0.924
Helper number	1	0.30	0.586	0.88	0.348
Pup sex	1	0.06	0.804	1.01	0.314
Litter size	1	0.01	0.903	0.24	0.621
Minimal model		Average effect	Standard error	Average effect	Standard error
Constant		-2.36	0.021	0.95	0.011
Bout location					
Open		0	0	0	0
Base of vegetation		0.10	0.0098	0.093	0.0097
Hole dug by other					
Yes		0	0	0	0
No		-0.095	0.016	-0.090	0.015
Pup age (days)				-0.0016	0.00045
Time of day					
AM				0	0
PM		-0.032	0.014		
Significant random terms (<i>P</i> < 0.05)			Territory, focal		Territory, litter, pup

Response terms (in seconds) were log transformed for analysis. Analyses were conducted on (A) 8047 foraging bouts and (B) 7324 unsuccessful bouts from 319 focal watches on 58 pups from 22 litters in 10 groups (mean = 5.5 ± 0.6 focal watches per pup, range = 1–15).

by adults may aid in this development. Pups' microhabitat choices became increasingly adult-like with age. Young pups seldom foraged at the base of vegetation, but the proportion of foraging bouts in this microhabitat increased with pup age, and for pups older than 65 days, it was not significantly different from that of adults in the group.

Changes in pups' microhabitat choices with age may occur in part due to positive reinforcement from prey capture. Young pups' foraging bouts were rarely successful, but success rates increased with age. Bouts conducted at the base of vegetation were significantly more likely to result in prey capture than bouts in the open. Prey capture may therefore act as a positive reinforcer, increasing the probability that pups would search for food in the same microhabitat type in future (Giraldeau 1984). Although there was no significant difference in the size of prey items pups found at the base of vegetation or in the open, among adults bouts at the base of vegetation produced prey of greater mass. This may provide an additional benefit to foraging in that particular microhabitat as pups' foraging skills improve.

The development of pups' microhabitat preferences is also likely to be affected by changes in searching behavior. Young pups spent little time searching for suitable places to dig before embarking on foraging bouts. Rather than moving slowly, with their nose oriented toward the sand and sniffing regularly, they moved with their head up and appeared to choose the location of foraging bouts haphazardly. However, as pups grew older, they spent significantly more time searching between foraging bouts. As a result, they may have been more likely to detect cues as to suitable microhabitats in which to dig. These cues may include prey odors or tracks and disturbed patches of sand. Patterns of digging also changed with age. Although there was no effect of age on overall bout duration, there was a negative effect when the analysis was restricted to unsuccessful bouts only,

suggesting that pups learn when to give up unproductive bouts through experience.

Microhabitat foraging choices may also be affected by social cues. Pups typically forage in close proximity to helpers (Brotherton et al. 2001; Hodge et al. 2007), and the average distance between pups and helpers increases as pups get older (Hollén and Manser 2006). As helpers commonly forage at the base of vegetation, proximity to helpers may increase the probability that pups conduct foraging bouts in that microhabitat. This suggestion is supported by the finding that the proportion of

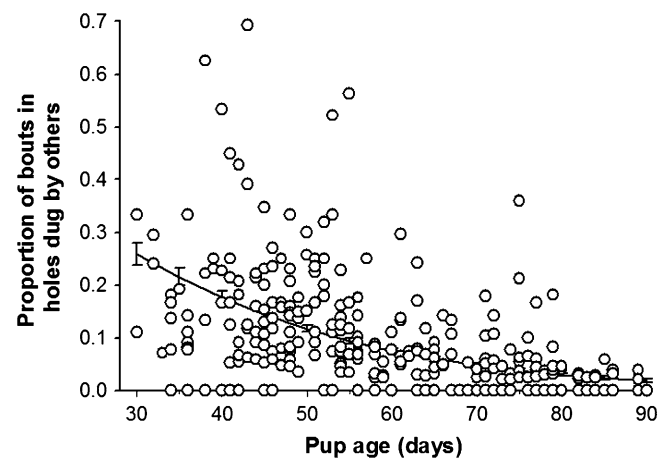


Figure 4
 The proportion of pup foraging bouts conducted in holes dug by other individuals declined with pup age (*P* < 0.001). Points show observed data; line is predicted means from a GLMM \pm standard error.

Table 5
GLMM on factors affecting the proportion of foraging bouts that pups foraged in holes previously dug by other individuals

Full model	Wald statistic (χ^2)	Degree of freedom	<i>P</i>
Pup age (days)	139.55	1	<0.001
Rainfall (mm)	8.53	1	0.003
Litter size	4.30	1	0.038
Pup age-corrected weight	0.31	1	0.577
Helper number	0.28	1	0.595
Time of day (AM, PM)	0.06	1	0.802
Pup sex	0.02	1	0.893
Minimal model	Average effect	Standard error	
Constant	-2.22	0.080	
Pup age (days)	-0.052	0.0044	
Rainfall (mm)	-0.0049	0.0017	
Litter size	-0.11	0.053	

Data were fitted to a binomial distribution with logit-link function with the number of foraging bouts in holes dug by adults during a focal watch fitted as the numerator and the total number of bouts fitted as the denominator. Analysis used data from 319 focal watches on 58 pups from 22 litters in 10 groups (mean = 5.5 ± 0.6 focal watches per pup, range = 1–15). Territory identity and litter constituted significant repeatability ($P < 0.05$), but individual and group identities were not significant random factors.

pup foraging bouts conducted at the base of vegetation increases with number of helpers in the group. Microhabitat choices may also be influenced by digging in holes dug by others. Helpers were never seen to dig in holes previously created by other individuals, despite the fact they often forage in close proximity to their group mates (Barnard 2000), suggesting that mature individuals actively avoid existing foraging holes. In contrast, young pups conducted around a quarter of their foraging bouts in holes dug by their elders. This proportion decreased as pups grew older, and pups from larger litters were less likely to forage in holes dug by helpers, presumably because of increased competition for access to helpers (Hodge et al. 2007). Foraging in existing foraging holes appeared to generate few direct nutritional benefits. Helpers were likely to have removed any prey that was present in the foraging hole, so bouts in existing holes were no more likely to result in prey capture than bouts in locations initiated by pups. When pups did find food in existing holes, it was more likely to consist of tiny items of small mass such as ant larvae left behind by the original hole digger. However, digging in holes dug by more experienced individuals may allow pups to obtain useful cues. When pups are young, their foraging bouts very rarely result in prey capture, so reinforcement of microhabitat choices through foraging success is lacking. However, by digging in holes dug by others, pups may encounter olfactory cues from prey items removed by the original hole digger. As helpers commonly dig at the base of vegetation, such cues may increase the probability that pups would dig in such locations again. A similar suggestion has been made for in a recent study on brown capuchin monkeys (*Cebus apella*), where the presence of bamboo segments left behind by others was found to raise the probability that young individuals would forage at bamboo stalks (Gunst et al. 2008).

The results of this study suggest that experience in early life affects the development of foraging microhabitat preferences in meerkats. Although the use of observational data cannot rule out the possibility that behavioral changes result from maturation or changes in food requirements alone, our results

strongly suggest an important role for learning. Young pups' foraging behavior appears haphazard, but as pups get older they spend more time searching for suitable locations in which to dig before embarking on a foraging bout. Positive reinforcement from prey capture may help pups to learn to dig in profitable microhabitats. Learning may be further facilitated through the use of social cues, particularly when pups are young and seldom find food themselves. Foraging in close proximity to helpers may raise the probability that pups will forage at the base of vegetation and cues gained from digging in holes dug by more experienced individuals may influence learning about the profitability of different microhabitats. Empirical and theoretical work suggests that in generalist species, adult tolerance of infants feeding from the same food source or scrounging scraps may promote learning about novel foods and handling techniques (Coussi-Korbel and Frigaszy 1995; Frigaszy et al. 1997; Lefebvre 1985). Social influences may also affect learning about the location of specific foraging patches and patch profitability (Galef and Giraldeau 2001; Galef 2003; Danchin et al. 2004). This study raises the possibility that tolerance of the close proximity of infants may also provide infants with cues that aid the development of foraging microhabitat choices. These cues may be integrated with information generated from individual experience to promote the establishment of adult-like microhabitat preferences. Such integration of personal and social information may be a common feature in the development of the foraging niche in generalist species.

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