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Effects of social learning on predator training and postrelease survival in juvenile black-tailed prairie dogs, *Cynomys ludovicianus*

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We examined how social context and experience affected development of antipredator behaviour and subsequent postrelease survival in the black-tailed prairie dog. Captive-reared juveniles were initially exposed to four stimulus animals: a ferret, a rattlesnake, a hawk and a cottontail control (pretraining tests). Subjects were then trained with or without an adult female demonstrator. Training involved exposure to each stimulus animal two to three times over 5 weeks. After training, each juvenile was retested with each stimulus animal (post-training tests). During pretraining tests, juveniles responded differentially to the stimulus animals. They were least active with the snake, fled the most in tests with the hawk, and were less vigilant with the ferret than with the snake. Following training, juveniles trained with experienced adults were more wary with all three predators than juveniles trained without an experienced adult present. We then compared the antipredator behaviour of captive-reared juveniles trained with experienced adult females with that of wild-reared juveniles of the same age. For all behavioural measures except shelter use, wild-experienced animals differentiated more strongly among predator types than did captive-trained juveniles. One year after reintroduction, survivorship of juveniles trained with experienced adults was higher than that of juveniles trained without experienced adults, but did not differ from that of wild-reared juveniles. These findings provide the first evidence that social transmission of antipredator behaviour during training can enhance long-term survival following release and that as long as a social training regime is used, predator avoidance training can emulate experience acquired in the wild.

Keywords: antipredator behaviour; black-tailed prairie dog; *Cynomys ludovicianus*; postrelease survival; predator avoidance; social learning

Social learning is important in the development of behaviour in many taxa (Zentall & Galef 1988; Heyes & Galef 1996; Galef & Laland 2005). Interactions with experienced conspecifics can allow inexperienced young to learn about their environment without incurring the time, energy and fitness costs associated with learning survival skills alone. For example, animals can modify their behaviour as a result of observing a conspecific responding to a stimulus (observational conditioning; Cook et al. 1985), or an experienced conspecific can indirectly bring the attention of a naïve animal to a particular stimulus or event in the local environment (local enhancement; Galef 1988). These mechanisms can lead to efficient development of effective foraging, mate selection and antipredator behaviour (Curio 1993; Brown & Laland 2001), and increase fitness (Mateo & Holmes 1997).

Social factors may strongly influence how experience shapes development. For example, in some songbirds, the presence of a live tutor can extend the developmental period during which species-specific song may be learned (Nordby et al. 2000) and even the presence of nonvocal

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social companions can affect song rate and potency (King et al. 2006). Similar processes may be evident in the acquisition of antipredator behaviour. Young animals may first encounter predators or predator-related stimuli in the company of their parents, siblings, or other conspecifics (Curio et al. 1978; Poran & Coss 1990). In Belding's ground squirrels, *Spermophilus beldingi*, juveniles living with their mother after natal emergence were able to discriminate between alarm and nonalarm calls faster than juveniles living without their mothers (Mateo & Holmes 1997). Fathers can also greatly influence the development of effective antipredator behaviour. In sticklebacks, *Gasterosteus aculeatus*, fry that are chased by their father, and that subsequently return to the nest, develop stronger avoidance responses towards a predator model than do fry that are orphaned (Huntingford & Wright 1993).

The degree to which adults influence the ontogeny of antipredator behaviour of their young is likely to vary with several factors. Extension of the period of parental care may increase the number of opportunities youngsters have to learn or otherwise benefit developmentally from their parents' antipredator behaviour (e.g. Cheney & Seyfarth 1990; Poran & Coss 1990). In highly social species, young animals may live and interact regularly with their own parents as well as other experienced adults (e.g. gregarious birds and colonial species). In many such species, several members of a group produce offspring at the same time and therefore show heightened vigilance associated with predators (Leger & Owings 1978). Juveniles raised in these groups may not be restricted to learning skills from their own parents, but rather may have the opportunity to learn life skills from other experienced and parentally motivated group members.

Information on the role of experience in the development of antipredator behaviour is of practical as well as theoretical importance when the subject species is the target of efforts to reintroduce captive-bred individuals into the wild (Kleiman 1989). Captive environments may fail to provide the predator-related experiences necessary to ensure survival upon release into native habitat, and even the skills of wild-caught individuals may erode during captivity (Kleiman 1989). Consequently, several recent studies have examined how animals learn to recognize and avoid predators (see reviews in Kelly & Magurran 2003; Griffin 2004), and predator training (e.g. providing critical predator-related experiences) is becoming part of many captive breeding programmes (Jarvi & Uglem 1993; McLean et al. 1996, 2000; Yoerg & Shier 1997; Griffin et al. 2000; Mirza & Chivers 2000; Brown & Laland 2001; Griffin 2004). But the success of such predator-training programmes depends on our understanding of the developmental processes supporting antipredator behaviour, and that understanding is quite limited (but see Miller et al. 1990; Yoerg & Shier 1997). To be most effective, antipredator training should mimic the critical features of ontogenetic processes in the wild: the experimental treatments used, the developmental timing of the training, and the social and physical context in which it occurs may all be crucial.

The primary goal of the present study was to investigate whether juvenile black-tailed prairie dogs trained in the presence of an experienced adult acquire more effective antipredator responses and thus higher survival postrelease than those trained in the absence of an experienced demonstrator. Black-tailed prairie dogs are prey to a variety of predators, including ferrets, raptors, snakes, coyotes, weasels and bobcats. Black-tailed prairie dogs are colonial and live in social groups called coteries, which typically contain one adult male, several adult females, yearling males and females, and juveniles (young of the year) (Hoogland 1995). Adult antipredator behaviour is well studied. Adult prairie dogs bark repetitiously, warning offspring and nondescendant kin of impending danger in the presence of mammals and aerial predators (Hoogland 1995). Upon hearing a bark alarm call, prairie dogs scan for predators, and if one is detected, they run to a burrow mound and either enter or begin calling (Hoogland 1995). Interactions with snakes are characteristically confrontational. Adult prairie dogs typically orient towards and approach the snake in an elongated posture, sniff, jump away and give distinct jump-yip calls and/or footdrum (Owings & Owings 1979; Owings & Loughry 1985). They also attack snakes (i.e. biting, swatting; Owings & Loughry 1985) and have been observed to throw substrate at them (Halpin 1983). Newly emergent juveniles remain close to burrows, are vigilant, and forage little (Loughry 1992). Juveniles jump-yip at higher rates upon emergence than they do in subsequent weeks (Loughry 1992), but they rarely bark or footdrum until they have been above ground for a few months (Hoogland 1995).

Social experience is probably essential for the development of antipredator behaviour in prairie dogs. Mothers call more often after the first juveniles emerge than do males or nonmaternal females (Hoogland 1995) and, therefore, may play an essential role in the development of effective antipredator behaviour. Newly emergent juveniles may benefit equally from all maternal females in their coterie since several females in a coterie may be reproductive at the same time and allonurse (Hoogland 1995). Newly emerged juveniles are highly vulnerable to predation, so individuals that can recognize life-threatening situations sooner may be more likely to escape from an otherwise fatal predator encounter.

This experiment was designed to determine: (1) whether newly emerged juvenile prairie dogs with no prior above-ground predator experience would show effective antipredator responses to three different predators following predator training with experienced adults (demonstrators); (2) whether trained captive-reared juveniles would behave similarly to wild-reared juveniles of the same age; and (3) whether juvenile prairie dogs trained with experienced adults (demonstrators) would show higher survival than juveniles trained without experienced adults 1 year after release.

METHODS

This experiment involved two groups of juveniles. Group 1 was trapped at emergence from their natal burrows and brought into captivity for experimental manipulation of predator experience (captive-reared). Group 2 comprised juveniles from the same coteries but they remained in the wild longer (trapped 7 weeks later; wild-experienced). Our first comparisons involved animals only from group 1; we compared the behaviour of captive-reared juveniles that were reared and trained with experienced adult demonstrators to the behaviour of captive-reared juveniles that were exposed to predators without experienced adults. Our second comparisons were between groups 1 and 2; we compared the behaviour of a subset of the captive-reared juveniles to the behaviour of a subset of the wild-reared juveniles. Finally, we released all juveniles (captive- and wild-reared) to the wild and assessed survival 1 year postrelease.

Experimental Manipulation of Predator Experience

Subjects and housing

Captive-reared subjects were 36 prairie dog juveniles born to eight females in the wild. These juveniles were live-trapped in 2001 on Vermejo Park Ranch, Colfax County New Mexico, within 1–2 days of emergence to prevent mixing of litters within a coterie. We trapped all juveniles in a litter along with their mother and transferred them to field enclosures on the property. To control for genetic variation, females and litters were collected from the same ($r = 0.5$) or neighbouring ($r > 0.375$) coteries (Hoogland 1995). Each female was housed with her litter in a separate wire-mesh enclosure ($2 \times 2 \times 3$ m) with a metal frame and a mesh canopy over the top. The mesh canopy prevented attacks by raptors but allowed exposure to other potentially important environmental cues (e.g. sun movement). Animals were provided with a burrow system of black PVC tubing and a wood nestbox ($0.3 \times 0.3 \times 0.5$ m), which was buried in 0.3 m of dirt to simulate natural burrow systems. Juveniles were dye-marked and eartagged for individual identification. Females and juveniles were allowed to habituate to the enclosures for 1 week prior to pretraining tests.

Experimental Protocol

Each focal juvenile was given a pretraining test (assessment of baseline antipredator behaviour), a 5-week training period involving two exposures to predators each week, and a post-training test. All tests were 10 min and occurred in the focal animal's home enclosure (Fig. 1).

Pretraining tests

At age 49 days (1 week following natal emergence), we measured each focal juvenile's ($N = 36$; one test/day) response to each of the following stimulus animals: (1) a live black-footed ferret, *Mustela nigripes*; (2) a live prairie rattlesnake, *Crotalus viridis*; (3) a moving, taxidermically mounted red-tailed hawk, *Buteo jamaicensis*; and (4) a live desert cottontail, *Sylvilagus auduboni*, as a nonpredator control.

During tests with the predators, the ferrets were active, often walking in the mesh box and oriented towards the focal prairie dog. The snakes were primarily coiled motionless near the barrier and oriented towards the prairie dog(s), unless detected. Cottontails were active and often foraged on grasses while in the mesh box.

Our testing methods were similar to those of Shier & Owings (2006) except that playbacks were not used in the present experiment and thus tests were not divided into periods. In general, we removed the mesh canopy from the top of the enclosure. We then removed all animals except the focal subject from the home enclosure to eliminate the effects of the social environment during exposure. We placed a mesh barrier or box in the home enclosure, and then allowed the focal subject to habituate to the testing conditions for 10 min. We then placed the test stimulus behind the barrier or in the mesh box (snake behind the barrier; ferret and cottontail in the mesh box). The observer then retreated to a blind 7 m from the enclosure and waited 2 min before starting the test to allow the focal subject to locate the stimulus animal. The hawk presentation is described in detail in Shier & Owings (2006). The order of stimuli was counterbalanced to avoid order effects. Each 10-min test was videotaped. An observer blind to treatment conditions scored the tapes.

Developmental conditions: training

Following the pretraining tests, we randomly assigned juveniles from each litter to one of three developmental treatments: (1) experienced adult (EA; $N = 18$), in which focal juveniles were reared and trained with their mother or a close female relative from their home coterie and their littermates; (2) alone ($N = 9$), in which focal juveniles were reared with their mother and littermates but exposed to stimulus animals alone; (3) sibling ($N = 9$), in which focal juveniles were reared and trained with inexperienced littermates. There were no main effects of treatment for any stimulus animal in the alone and sibling treatments, so we ruled out rearing as a confounding factor and focused our analysis on the effects of training juveniles with and without an experienced adult present. Thus, we combined the 'alone' and 'sibling' treatments into one treatment, 'without experienced adults' (WEA), where juveniles were trained without an experienced adult present. Training periods were 10-min sessions in which either the ferret, snake or cottontail was placed behind the mesh barrier or in the mesh box in the focal prairie dog home cage, or the hawk was presented via a pulley system midway through the session. Once juveniles were assigned to a treatment, they remained in that treatment condition for the duration of the experiment. Each juvenile from the three treatments was exposed to the ferret and the hawk two times and the rattlesnake and the cottontail three times during the 5-week period (two exposures/week). Rattlesnakes and cottontails are more common to prairie dog colonies and thus juveniles were given an additional exposure to each of these stimulus animals to replicate the natural variation in exposure in the wild. To control for possible sex differences, we divided the number of male and female juveniles from each litter equally among the two groups.

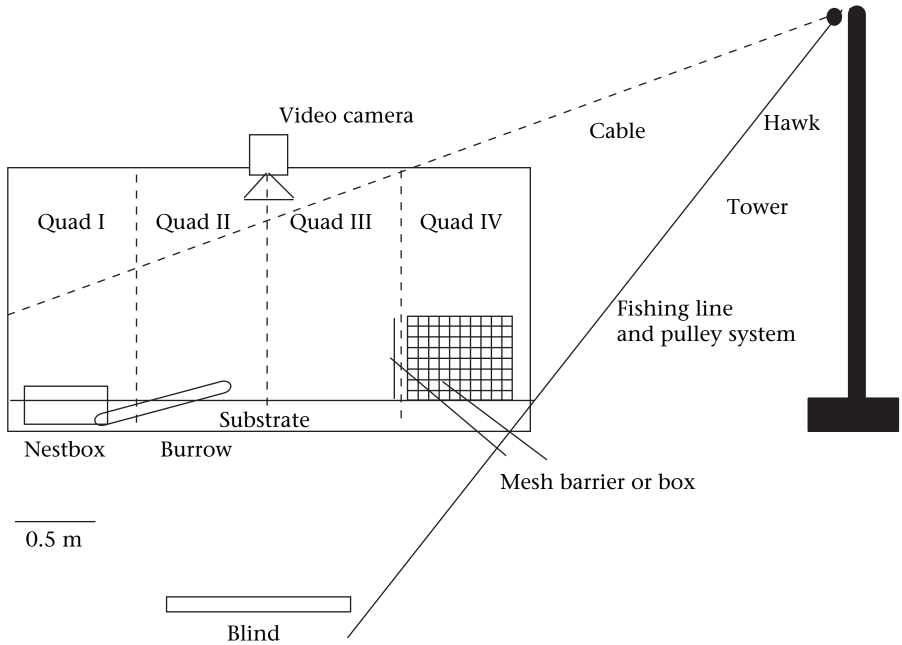

Figure 1. Test enclosure set-up. Live stimulus animals were presented in quadrant IV, either behind the mesh barrier (snake) or in the mesh box (cottontail, ferret). A taxidermic mount of a hawk was presented using the line and pulley system. During stimulus presentations, prairie dog subjects had access to quadrants I–III (snake) or to quadrants I–IV (cottontail, ferret, hawk). The experimenter sat behind the blind during testing. (Modified from Shier & Owings 2006).

Post-training tests

To measure the change in behaviour, if any, due to predator exposure, we tested each focal juvenile after the 5-week treatment period with each type of predator and the nonpredator stimulus. The post-training tests followed the same procedures as the pretraining tests. To minimize the problem of pseudoreplication, we used three exemplars of each stimulus animal. A different exemplar of each stimulus animal was used during each of the pretraining, training and post-training tests such that each focal animal was presented with three different exemplars during the course of the experiment.

Comparison to wild-reared counterparts

Once post-tests were complete, all remaining coterie members in the wild were trapped and brought into the enclosures ($N = 14$ adult males, 19 adult females, 14 juvenile males, 16 juvenile females). The newly trapped prairie dogs were given 1–3 days to habituate to the enclosures. We tested a subset of these wild-reared juveniles (four males, five females) with each stimulus animal following the same procedures for the pretraining tests and compared their behaviour to that of EA juveniles.

Analysis of Behavioural Responses

We quantified the following five behaviours to measure the effect of social context on predator training in juvenile prairie dogs: (1) vigilance (seconds/10-min test); (2) antipredator vocalizations (calls/min); (3) shelter use (seconds/10-min test); (4) activity (number of quadrant changes/min; see Fig. 1); (5) fleeing (occurrences/min), as described in Shier & Owings (2006).

Two animals from the WEA treatment were removed from testing because of injuries sustained while they were in the enclosure. Thus, data analyses are based on a sample size of 34 juvenile prairie dogs. We used *t* tests for each dependent variable to test for sex differences in behaviour in the pretraining test and again in the post-training test. All *t* tests were statistically nonsignificant at an alpha level of 0.05 (Student's *t* test: pretraining tests: vigilance: $t_{134} = 1.322$, $P = 0.189$; vocalization: $t_{134} = -0.906$, $P = 0.367$; shelter: $t_{134} = -0.583$, $P = 0.561$; activity: $t_{134} = 0.708$, $P = 0.480$; post-training tests: vigilance: $t_{134} = 0.219$, $P = 0.827$; vocalization: $t_{134} = -0.366$, $P = 0.715$; shelter: $t_{134} = -1.394$, $P = 0.166$; activity: $t_{134} = 0.708$, $P = 0.480$). Therefore we combined males and females in subsequent analyses and did not include sex as a factor. We analysed pretraining tests using one-way ANOVAs with stimulus type (ferret, hawk, snake, cottontail) as a within-subjects factor and we used Bonferroni corrected pairwise comparisons to examine differences in responses to each predator type and control.

Because prairie dogs behaved differently in the presence of different predator types during pretests, we conducted statistical analyses for each predator type separately (ferret, hawk, snake, cottontail). Therefore, to examine the effects of social context on training, for each predator, we computed the change in each focal juvenile's behaviour from pre- to post-training (post-training minus pretraining test behaviour) and performed a two-factor ANOVA with developmental treatment (EA versus WEA) and litter as the between-subjects variables. There were no main effects of litter, so we removed it from the final model and reanalysed the data using a one-factor ANOVA.

To determine whether vigilance and alarm calling levels of demonstrators ($N = 8$) were correlated with juvenile prairie dog behaviour, we randomly selected one training period with each type of stimulus animal for each EA juvenile and determined the demonstrator's frequency of alarm calling and amount of time spent vigilant. We used a Pearson's product–moment correlation to determine whether juveniles' responses during post-training tests were correlated with these aspects of demonstrators' behaviour during training.

To investigate differences in behaviour between wild-reared and captive-reared juveniles trained with experienced adults, we compared the behaviour of EA juveniles during post-training tests to that of wild-reared juveniles of the same age using a two-factor mixed ANOVA with rearing condition (wild-reared versus captive-reared) as the between-subjects factor and predator type (ferret, hawk, snake) as the within-subjects factor. Juveniles behaved differently with the cottontail control stimulus during the post-training tests, so we compared the behaviour of wild-reared and trained captive-reared juveniles during tests with the cottontail separately using a *t* test for each dependent variable. All statistical analyses were conducted using SPSS version 13 for Windows (SPSS Inc., Chicago, Illinois, U.S.A.).

Measuring Training Success

At the end of the experiment all subjects (captive-reared, $N = 34$; wild-reared, $N = 30$) and all adults and littermates from their coteries were released in a newly established prairie dog colony to measure survival and reproductive success. We used a 'soft release' protocol established by Truett & Savage (1998), which allowed the animals to habituate to the new site and remain protected from predators while digging new burrow systems. Coterie units were kept together to decrease stress and reduce postrelease dispersal (see Truett & Savage 1998; Shier 2006).

We compared survivorship of captive-reared, trained and reintroduced juveniles to that of wild-reared and translocated juveniles the following spring, 2002, to determine whether the survival rate of animals reared and trained in captivity differed from that of translocated animals from the same coteries.

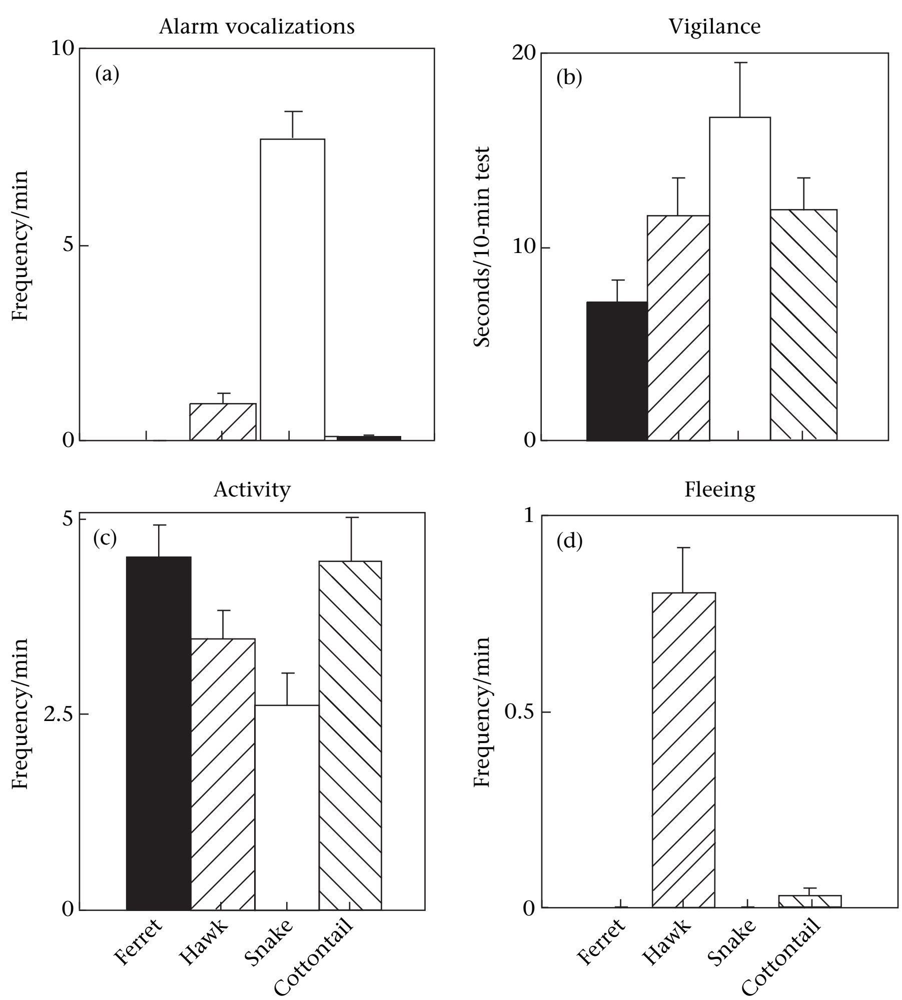

Figure 2. Effects of stimulus type (ferret, hawk, snake, cottontail) on antipredator behaviour of newly emerged juvenile prairie dogs during pretraining tests. (a) Antipredator vocalizations; (b) vigilance; (c) activity; (d) fleeing. Means + SEs are shown.

RESULTS

Pretraining Tests

On first presentation, newly emerged juvenile prairie dogs behaved differently towards the four stimulus animals (Fig. 2). Juveniles' responses to predator and nonpredator stimulus animals differed significantly for all behavioural measures except shelter use (ANOVA: main effect of predator: activity: $F_{3,132} = 4.093$, $P = 0.008$; vigilance: $F_{3,132} = 3.001$, $P = 0.033$; vocalizations: $F_{3,132} = 76.173$, $P = 0.0001$; fleeing: $F_{3,132} = 4.149$, $P = 0.008$; shelter use: $F_{3,132} = 2.517$, $P = 0.061$; Fig. 2). Juveniles were significantly less active (Bonferroni corrected pairwise comparison: $P = 0.025$) and spent significantly less time vigilant (oriented towards and alert; $P = 0.04$) in the presence of the ferret than in the presence of the snake. The hawk elicited the most fleeing behaviour (Bonferroni corrected pairwise comparison: versus ferret: $P = 0.025$; versus cottontail: $P = 0.036$; versus snake: $P = 0.025$), while the snake elicited the most alarm vocalizations (versus ferret: $P = 0.0001$; versus hawk: $P = 0.0001$; versus cottontail: $P = 0.0001$).

Effect of Social Context on Training

The presence of an experienced adult demonstrator during training influenced responses of juveniles during testing (Fig. 3). In general, juveniles that had been trained with an experienced adult were more wary of the three predator stimulus animals than were juveniles that had been trained without an experienced demonstrator, but

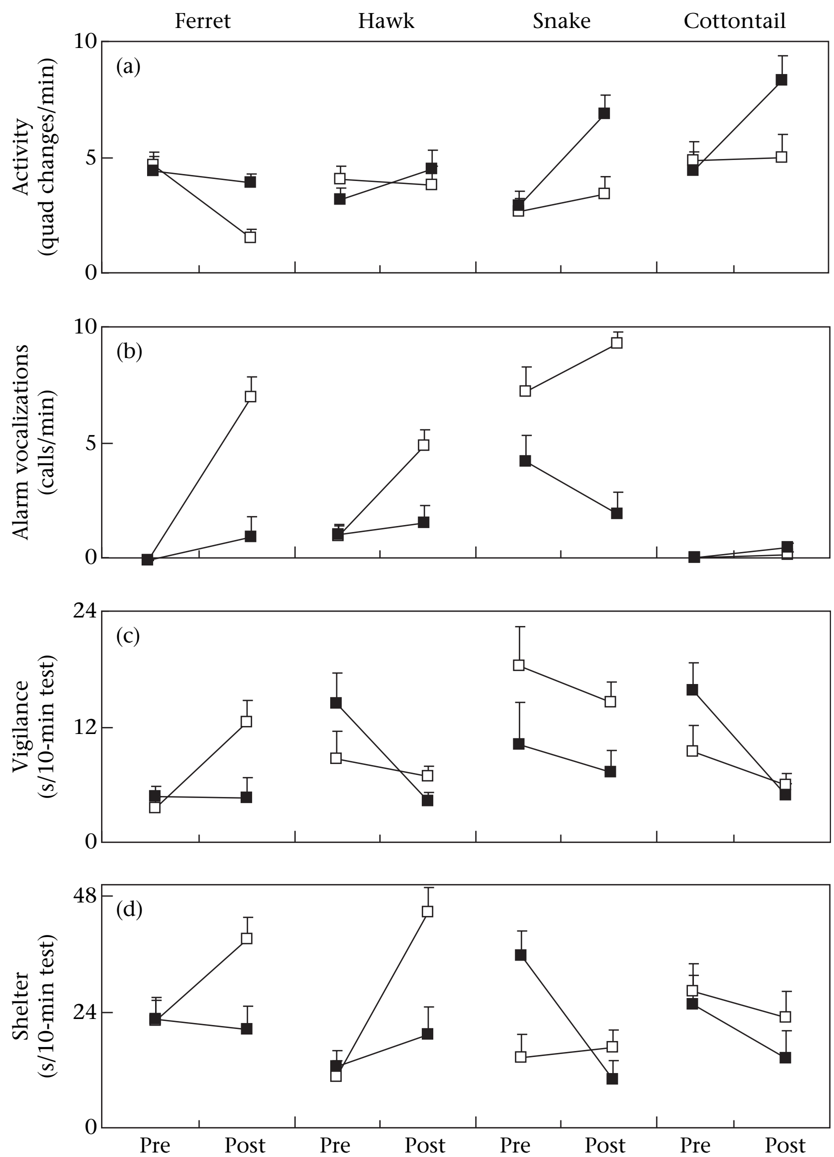

Figure 3. Effects of social context during training on post-training responses of captive-trained juvenile prairie dogs to four stimulus animals (ferret, hawk, snake, cottontail). (a) Activity; (b) antipredator vocalizations (barking and jump-yipping); (c) vigilance; (d) shelter use. Mean rates of behaviour (duration or frequency/min) + SEs are shown. □: juveniles trained with experienced adults (EA, $N = 18$); ■: juveniles trained without experienced adults (WEA, $N=16$). All juveniles were tested alone.

Table 1. Treatment effects for captive-reared juveniles

Stimulus animal	ANOVA factor: Treatment (EA versus WEA) $F_{1,32}$	P	Effect size: Parial eta-squared
Ferret			
Vigilance	6.810	0.014	0.175
Shelter	4.910	0.034	0.133
Bark vocalizations	24.306	0.000	0.432
Activity	4.576	0.040	0.125
Hawk			
Vigilance	4.257	0.047	0.117
Shelter	10.725	0.003	0.251
Bark vocalizations	7.694	0.009	0.194
Activity	2.411	0.130	0.070
Snake			
Vigilance	0.018	0.893	0.001
Shelter	2.871	0.137	0.262
Jump-yip vocalizations	7.531	0.010	0.191
Activity	14.961	0.000	0.131
Rabbit			
Vigilance	3.273	0.080	0.093
Shelter	0.278	0.602	0.009
Bark vocalizations	2.105	0.157	0.062
Activity	6.508	0.016	0.169

Results of one-way (treatment) ANOVAs comparing the mean rate of change (duration or frequency/min) of behaviour from pre- to post-training (post-training minus pretraining tests) by juvenile prairie dogs in tests with each stimulus animal. EA: juveniles reared and trained with experienced adults; WEA: juveniles reared and trained without experienced adults.

no such effect of demonstrators was evident for the control stimulus.

During exposure to the ferret, there were significant effects of treatment for all four dependent measures. From pre- to post-training, juveniles trained with experienced demonstrators decreased activity and increased alarm vocalizations and the time that they allocated to vigilance and shelter. In contrast, juveniles trained without experienced demonstrators showed no change in any behaviour from pre- to post-training with the ferret (Table 1, Fig. 3).

In the presence of the hawk, juveniles trained without experienced demonstrators decreased time allocated to vigilance from pre- to post-training, whereas juveniles trained with experienced demonstrators did not (Table 1, Fig. 3). There was an overall increase in bark vocalizations and time spent in shelter following training (ANOVA intercept: bark vocalization: $F_{1,32} = 16.257$, $P < 0.0001$; shelter: $F_{1,32} = 23.677$, $P < 0.001$), although this effect was much more pronounced for EA juveniles than for WEA juveniles (Table 1, Fig. 3).

In tests with the snake, EA juveniles increased the frequency of alarm vocalizations from pre- to post-training tests, but showed no significant change in activity or time allocated to shelter. In contrast, juveniles trained without experienced adult demonstrators increased activity and decreased alarm vocalizations and time spent in shelter following training (Table 1, Fig. 3).

Finally, in tests with the cottontail (control stimulus), WEA juveniles showed a striking increase in activity from pre- to post-training, whereas activity levels of EA juveniles did not differ from pre- to post-training (Table 1, Fig. 3). Frequency of alarm vocalizations, time allocated to vigilance and time spent in shelter did not differ from pre- to post-training with the cottontail (Table 1, Fig. 3).

Relationship to Demonstrator Behaviour

During training, the vigilance behaviour and alarm vocalizations of juveniles closely followed those of the experienced demonstrator prairie dogs with which they were housed. Formal analysis revealed that the behaviour of juveniles during post-training tests was significantly correlated with demonstrator behaviour during training (Pearson's correlation: vigilance: $r_{106} = 0.854$, $P < 0.001$; alarm vocalizations: $r_{106} = 0.421$, $P < 0.001$).

Captive-trained versus Wild-experienced Juveniles

Juveniles reared in captivity and trained with experienced adult females behaved differently during post-training tests than juveniles of the same age reared in the wild (Table 2, Fig. 4). In general, wild-experienced

Table 2. Comparisons between captive-reared juveniles trained with an experienced adult and wild-experienced juveniles

Comparison	Rearing condition $F_{1,25}$	P	Effect size*	Predator type $F_{2,50}$	P	Effect size*	Rearing×predator $F_{2,50}$	P	Effect size*
Captive-trained versus wild-reared									
Vigilance	8.545	0.007	0.255	19.140	0.000	0.434	13.029	0.000	0.343
Shelter	10.134	0.004	0.288	11.590	0.000	0.317	1.197	0.311	0.046
Alarm vocalizations	12.625	0.002	0.336	7.942	0.000	0.241	3.915	0.026	0.135
Activity	0.360	0.554	0.014	24.918	0.000	0.499	19.600	0.000	0.439

Results of two-way (rearing × predator type) repeated measures ANOVAs comparing the mean time or frequency allocated to four behaviours by the two groups of juveniles.
*Effect size is given in partial eta-squared.

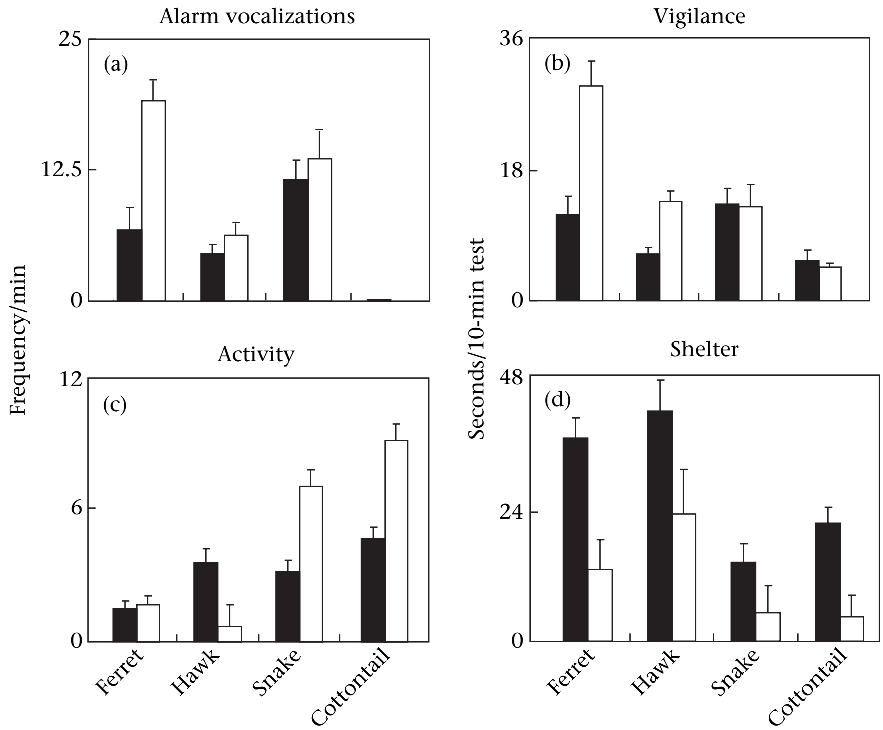

Figure 4. Effects of rearing condition (captive-reared and trained with experienced adults (■) versus wild-reared (□)) and stimulus type (ferret, hawk, snake, cottontail) on behaviour. (a) Alarm vocalizations; (b) vigilance; (c) activity; (d) shelter use. Data for captive-reared and trained animals are from post-training tests. Mean rates of behaviour (duration or frequency/min) + SEs are shown.

juveniles were more wary, alarm calling and allocating more time to vigilance, but spending less time in shelter than captive-trained juveniles (Table 2, Fig. 4). Overall, juvenile prairie dogs behaved differently in the presence of different predators (Table 2), and more specifically, the results suggest that captive-reared and wild-reared juveniles do not differentiate among the predators in the same way (Table 2). For nearly all measures except shelter use, wild-experienced juveniles differentiated more strongly among predator types than did captive-trained juveniles (Table 2, Fig. 4). In the case of activity, there was also a quantitative difference in how wild-experienced and captive-trained juveniles responded. Wild-experienced juveniles were less active than captive-trained juveniles in trials with the hawk (Student's t test: $t_{25} = 2.439$, $P = 0.022$), but more active when tested with the snake ($t_{25} = -4.359$, $P = 0.001$). Finally, when tested with the cottontail control, wild-reared juveniles were more active and spent less time in shelter than captive-reared juveniles trained with experienced adults (activity: $t_{25} = -2.899$, $P = 0.008$; shelter: $t_{25} = 2.245$, $P = 0.034$).

Training Success

Social context and rearing condition affected survival following release. Juveniles reared and exposed to predators in the presence of an experienced adult female from their home coterie were more likely to survive for 1 year postrelease than were juveniles trained without an experienced adult (chi-square test: $\chi^2_{33} = 5.7$, $P = 0.017$; Fig. 5). Juveniles reared in the wild and translocated to a new site were significantly more likely to survive 1 year postrelease than were juveniles reared in captivity, trained with predators, and reintroduced (chi-square test: $\chi^2_{63} = 3.979$, $P = 0.043$; Fig. 5). However, survivorship of wild-reared juveniles and of juveniles reared and trained in captivity with experienced adults did not differ (chi-square test: $\chi^2_{47} = 0.119$, $P = 0.732$; Fig. 5).

DISCUSSION

Our results show that, at emergence, juvenile prairie dogs differentiate among predators. During initial exposure to the three predators and the cottontail control, juveniles were less active and more vigilant in the presence of the rattlesnake than in the presence of the ferret, they alarm-called the most during interactions with the rattlesnake, and they showed fleeing behaviour almost exclusively in the presence of the hawk. The differences in alarm behaviour with the different predator types suggest that the immediate pattern of stimulation presented by each predator influences the alarm behaviour of juvenile prairie dogs. Snakes are ambush predators that rely on stealth, rather than speed, and they prey primarily on relatively young prairie dog pups (i.e. pre- and newly emerged juveniles; Loughry 1987; Shier 2006). Like young ground squirrels, *Spermophilus beecheyi*, newly emerged prairie dogs may show adult-like defensive behaviours in the absence of experience with snakes (Owings & Coss 1977; Poran & Coss 1990). However, because snakes enter burrows before juvenile emergence, some juveniles may have had experience with snakes

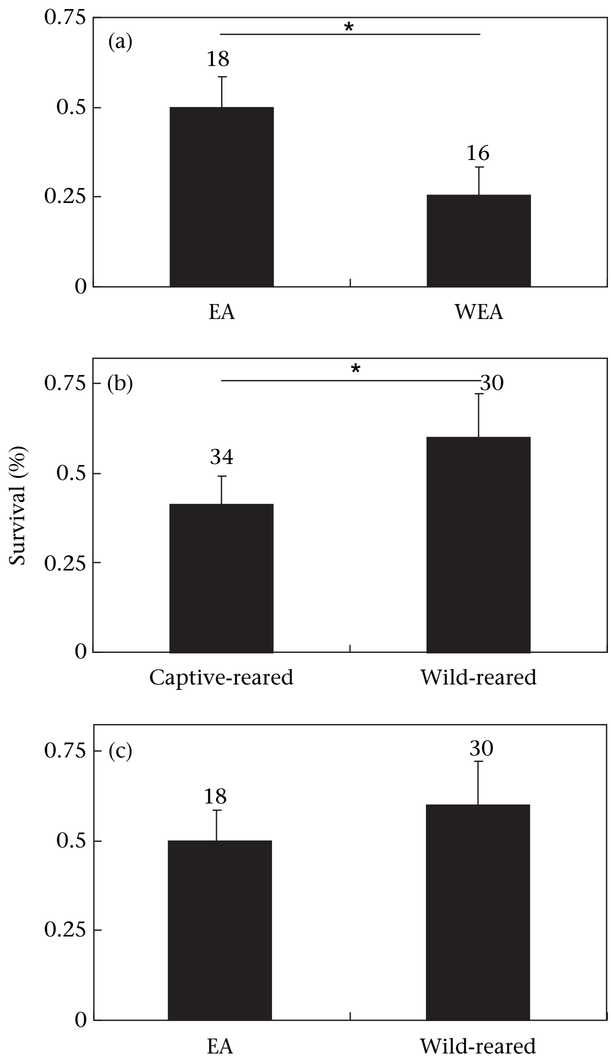

Figure 5. Differences in mean + SE survival of juveniles (a) trained with experienced adults (EA) versus trained without experienced adults (WEA), (b) captive-reared and reintroduced versus wild-reared and translocated and (c) captive-reared and trained with experienced adults (EA) versus wild-reared. Means + SEs are shown. Sample sizes are indicated above bars. *$P < 0.05$.

before testing, which could explain pretest differences between EA and WEA juveniles if such snake experience was incidentally confounded with this experimental manipulation. While it is unlikely that juvenile prairie dogs had any prior experience with hawks, ferrets or cottontails since they were trapped at emergence, hawks were a looming threat that may not require experience to elicit avoidance behaviour (Giles 1984; Hanson & Coss 1997). Not surprisingly, newly emerged juveniles fled away from the flying hawk. Juvenile prairie dogs did not behave differently in tests with ferrets and cottontails at emergence, suggesting that distinction between these animals requires some form of experience or learning after emergence.

Our findings may provide the first demonstration of social conditioning in a rodent. Antipredator behaviour was socially transmitted to predator-naïve juveniles. Juvenile prairie dogs that were trained with experienced adults from their home coterie were more wary during subsequent exposure to predator and nonpredator stimulus animals than were juveniles trained without experienced demonstrators. Following training with experienced adults, juveniles alarm-called more frequently, were more vigilant, showed reduced activity and spent more time in shelter in the presence of all four stimulus animals than did juveniles trained without experienced adults. Furthermore, levels of vigilance and alarm vocalizations of demonstrators during training were correlated with juvenile prairie dog behaviour during the post-training tests. This pattern of results suggests that juvenile prairie dogs attended to the behaviour of the demonstrator, if present, and that this altered their subsequent responses to the test stimuli.

Does training young prairie dogs in captivity elicit antipredator behaviour similar to that of animals that have had experience in the wild? The results suggest it does not. Prior to release, trained captive-reared juveniles spent less time vigilant and alarm calling and more time in shelter than wild-reared juveniles of the same age. These differences are most likely due to different environments during development. Disparity in the amount of time that juveniles spent in shelter may be due to differential exposure to the enclosure itself. However, differential acclimation to the enclosure cannot fully explain the higher rates of alarm calling or vigilance shown by the wild-reared juveniles because these behaviours varied by predator type and therefore do not represent an overall heightened reactivity. Rather, these differences were probably due to critical features of the juvenile's social and physical environments during development. For example, wild-reared juveniles had the opportunity for above-ground experience with predators in the presence of multiple group members.

For individuals that live in stable groups, such as prairie dogs, a social group, rather than the individual or a single additional social partner, form the backdrop for social learning (Heyes & Galef 1996), and social training regimes are likely to be more effective because they mimic natural processes. Not surprisingly, research has begun to reveal the various influences of social context (number of demonstrators: Galef & Whiskin 1997; Leland & Williams 1997; demonstrator status: Drea & Wallen 1999; Nicol & Pope 1999) and housing environment (Beecher 1996; Tchernichovski & Nottebohm 1998) on learning, and suggests that what an individual learns will depend on the context in which it is presented. In this study, naïve juveniles were exposed to predators with only one demonstrator present. It is possible that the behavioural differences between captive and wild-reared individuals were simply due to the number of demonstrators present during interactions with predator stimuli. Alternatively or in addition, the complex interactions between multiple individuals and their environment may be required for the development of appropriate skills. It seems reasonable to assert that watching or hearing fearful behaviour or smelling pheromones released during interactions of nearby individuals has contagious properties (see de Gelder et al. 2004). These types of interactions were not faithfully replicated in this captive setting. Further studies examining the effectiveness of predator training in the presence of intact social groups may shed light on this dynamic process.

Finally, prerelease training appears to enhance postrelease survival. Shier & Owings (2006) showed that prerelease training with predators increased survival of juvenile prairie dogs following release. The present study provides the first evidence that social transmission of antipredator behaviour during training can enhance long-term survival following release. Juveniles trained with experienced demonstrators while in captivity were more likely to survive 1 year postrelease than those exposed to predators without experienced demonstrators. Perhaps more importantly, the results further suggest that predator avoidance training can emulate experience acquired in the wild, as long as a social learning regime is used. While wild-reared juveniles translocated to the same site were more likely to survive than trained captive-reared juveniles, there was no difference in the survival of juveniles that were brought into captivity at emergence and trained with experienced adult demonstrators and those that were wild-reared and translocated. These results encourage further investigation into the application of social experience and/or learning in predator training, particularly for species in which captive breeding is the only viable alternative.

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