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Snake scent application in ground squirrels, *Spermophilus* spp.: a novel form of antipredator behaviour?

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Chemical substances produced by one species are sometimes found on the body of another species. Animals often ingest such foreign substances and sequester them into their integument, but here we report a case of direct application of heterospecific substances to the body. California ground squirrels, *Spermophilus beecheyi*, and rock squirrels, *Spermophilus variegatus*, apply scent derived from their major predator, rattlesnakes, *Crotalus* spp., by chewing shed rattlesnake skins and licking their fur. We found that the sequence of body areas licked during application was essentially the same for the two species. We consider three hypotheses regarding the function of this 'snake scent application' (SSA): antipredator defence, ectoparasite defence, and conspecific deterrence. To test these hypotheses, we assessed patterns of species and sex/age class differences in application quantity and compared them with patterns reflecting differences in the importance of predation, flea loads and conspecific aggression as sources of selection. We found no species differences in application quantity; however, juveniles and adult females of both species engaged in longer bouts of application than adult males. This pattern of sex/age class differences in SSA supports only the antipredator hypothesis because juveniles are most vulnerable to predation and adult females actively protect their young. We found no evidence to support either the ectoparasite defence or conspecific deterrence hypotheses. Thus, SSA behaviour may be a novel form of chemical defence against predation.

Keywords: antipredator behaviour; chemical defence; *Crotalus*; ground squirrel; rattlesnake; rock squirrel; *Spermophilus*; stereotyped behaviour

Animals opportunistically use resources in their environment for novel purposes, such as tools or material for nest construction (Lestel & Grundmann 1999). In some cases, the commandeered substances are produced by other animal species (e.g. Williams et al. 2004). Certain amphibian and avian species, for example, acquire chemicals from ingested prey and sequester them into their integument (Daly 1997; Bartram & Boland 2001). Other animals, representing a wide array of taxa, directly apply foreign substances onto their integument, an activity called 'self-application' or 'anointment' (Weldon 2004; see Table 1).

Chemicals sequestered internally by animals are typically thought to reduce the animals' palatability to predators. Consistent with this hypothesis, animals that sequester toxic chemicals are often aposematic (e.g. Dumbacher & Fleischer 2001). In contrast, many species that directly apply substances to their skin lack conspicuous coloration and use substances that are odiferous rather than toxic (see Table 1). Thus, self-applied chemicals might be used by the applier in different ways than chemicals sequestered internally. Indeed, several studies have proposed that odorous applied substances repel predators and/or ectoparasites (Kobayashi & Watanabe 1986; Xu et al. 1995; Weldon et al. 2003; Weldon 2004; Carroll et al. 2005) or

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Table 1. Examples of applied substances and proposed functions

Proposed function	Substance source	Applier	Application behaviour
Antipredator	Snake	Chipmunks[1]	Chew on snake carcass and apply by licking into fur
Antipredator	Weasel	Rats[2]	Chew filter paper saturated with weasel anal gland secretions and apply by licking into fur
Antipredator (social)	Toad	Hedgehogs[3]	Chew toad skin then apply by licking into fur
Antipredator	Brown algae	Decorator crabs[4]	Cover carapace with algae
Ectoparasite defence	Ants	Birds[5]	Sit on ant mound and/or bite ant(s) and apply to feathers with beak
Ectoparasite defence	Millipedes	Birds[6]	Bite millipede and apply to feathers with beak
Ectoparasite defence	Millipedes	Primates[7]	Bite millipede and rub secretions into fur
Ectoparasite defence	Leaves	Primates[8]	Rub chewed leaves into fur
Ectoparasite defence	Catnip	Felines[9]	Roll on catnip
Ectoparasite defence	Tree resin	Coatis[10]	Dig claws into resin seeping from tree and apply to fur
Social	Carcasses	Hyaenas[11] Wolves[12]	Roll on prey carcass
Integration into an ant colony	Ants	Beetles[13]	Cover carapace with dead ants
None given	Ants	Grey squirrels[14]	Roll around on ants and/or ant hills

1. Kobayashi & Watanabe 1986; 2. Xu et al. 1995; 3. Brodie 1977, D'Have et al. 2005; 4. Stachowicz & Hay 1999; 5. Clark 1990, Fauth et al. 1991, Husak & Husak 1997, Rodgers et al. 1998, Osborn, 1998, Milton & Dean 1999, Craig 1999, Gwinner et al. 2000; 6. Harrup 1992, Parkes et al. 2003; 7. Birkinshaw 1999, Valderrama et al. 2000, Zito et al. 2003, Weldon et al. 2003; 8. Baker 1996, Campbell 2000, Zito et al. 2003; 9. Tucker & Tucker 1988, Bernier et al. 2005; 10. Gompper & Holyman 1993; 11. Drea et al. 2002; 12. Zimen 1981; 13. Vandermeer & Wojcik 1982; 14. Bagg 1952, Hauser 1964.

affect the behaviour of conspecifics (Kobayashi 2000; Drea et al. 2002; D'Have et al. 2005).

Several rodent species apply substances acquired from their snake predators by chewing the source (e.g. shed skins, carcasses) and licking their fur. This behaviour, termed 'snake scent application' (SSA), was first reported in Siberian chipmunks, *Eutamias sibericus asiaticus* (Kobayashi & Watanabe 1986) and was later observed in some ground squirrels, *Spermophilus* spp. (Owings et al. 2001) and grasshopper mice, *Onychomys torridus* (M. Rowe, unpublished data). Similarly, rice-field rats, *Rattus rattoides*, chew on and apply the anal gland secretions of weasels, *Mustela sibirica*, a rodent predator, (Xu et al. 1995). This behaviour in these rodent species appears similar to the phylogenetically conserved head-to-tail (cephalocaudal) grooming sequence (see Berridge 1990), suggesting an evolutionary derivation from this grooming sequence. Here we evaluate the form of SSA in two ground squirrel species by presenting California ground squirrels, *S. beecheyi*, and rock squirrels, *S. variegatus*, with shed skins from local rattlesnake species, *Crotalus* spp. (Fig. 1) and quantifying the sequence and location of application to different body areas.

Predator scent application has been proposed to serve an antipredator function (Kobayashi & Watanabe 1986; Xu et al. 1995), but alternative explanations are also plausible. We consider three functional hypotheses of SSA in ground squirrels: antipredator defence, ectoparasite defence, and conspecific deterrence. We test these hypotheses by comparing patterns of species and sex/age class differences in amount of application with patterns reflecting differences in importance of predators, flea loads and conspecific aggression. Contrasting patterns of selection from these three sources both between the two species and among different age and sex classes of squirrels can provide insights into the function of SSA.

Both of the closely related (Herron et al. 2004) but geographically separate ground squirrel species studied here have been subjected to rattlesnake predation for many millennia (Coss 1999), which has led to the evolution of a complex defence system that includes venom resistance in adults and sophisticated antisnake behaviour (Owings & Coss 1977; Rowe & Owings 1978; Hennessy & Owings 1988; Biardi 2000; Owings et al. 2001). However, California ground squirrels live at higher densities than rock squirrels (compare Fitch 1948 with Shriner & Stacey 1991) and show greater sexual differentiation in size (Owings et al. 2001) and apparently aggressiveness. In addition to age/sex class differences in the impact of predators, ectoparasites and conspecifics (Fitch & Twining 1946; Owings et al. 1979; Bursten et al. 1997), we use these species differences to make predictions for each functional hypothesis.

Antipredator

SSA might alter ground squirrel odour and thereby either reduce detectability to predators or repel other rattlesnakes motivated to avoid hunting in the same area as a conspecific. Juvenile ground squirrels are the most susceptible to predation, especially from rattlesnakes because their small size limits the volume of venom they can neutralize, and because they are less likely to evade predators (Fitch & Twining 1946; Owings & Coss 1977; Poran et al. 1987; Mateo, 2007). Nevertheless, adult females actively protect their offspring from rattlesnakes (e.g. Swaisgood et al. 2003), share burrows with vulnerable related juveniles (Johnson 1981; Boellstorff & Owings 1995), and generally deal more directly with predators than do adult males (e.g. through alarm calling; Dunford 1977; Sherman 1977; Schwagmeyer 1981). Therefore, we predicted that juveniles and adult females would SSA more than adult males in both species if it serves an antipredator function.