

# Grooming in Impala: Role of Oral Grooming in Removal of Ticks and Effects of Ticks in Increasing Grooming Rate

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MOORING, M. S., A. A. MCKENZIE, AND B. L. HART. *Grooming in impala: Role of oral grooming in removal of ticks and effects of ticks in increasing grooming rate.* *PHYSIOL BEHAV* 59(4/5) 965–971, 1996.—In Experiment 1, five adult female impala were fitted with harnesses that restrained oral self-grooming of the anterior part of the body. At the same time, six cohoused female impala were fitted with control harnesses that allowed normal oral grooming. The impala were allowed to habituate to the harnesses for 10 days, and both groups were then exposed to larval ticks (*Boophilus decoloratus*) by herding them into a tick-seeding corral. During the third week following tick seeding, when female ticks were estimated to have developed into engorging adults, the impala were immobilized, tick numbers on the animals sampled by patch sampling, and the harnesses removed. Observations continued for 5 days following removal of the harnesses. Twenty-minute focal observations were conducted daily on each impala during the habituation, tick-seeded, and postharness phases. Restrained impala had a median of 20 times more adult female ticks (both engorged and unengorged) than control impala. Oral grooming, which had been suppressed in the restrained impala during habituation and tick-seeded phases, increased 10-fold once the harnesses were removed and occurred 2.5 times more frequently than in control impala during the postharness phase. In Experiment 2, 15 adult female impala were seeded with larval ticks as in Experiment 1; in week 3 after tick seeding all ticks were removed from animals by application of an acaricide. Grooming was recorded during 3 weeks of baseline observations prior to tick seeding, 3 weeks after tick seeding, and then for 3 weeks beginning 1 week after acaricide treatment. Oral grooming and scratch grooming significantly increased from baseline during tick seeding and significantly declined following removal of the ticks with acaricide. Taken together, the two experiments demonstrate that oral grooming is very effective and important in removing fitness-compromising ticks in free-ranging impala. Correspondingly, exposure to, and subsequent infestation by, ticks increases the rate of grooming.

Grooming      Impala      Ixodid ticks      Parasite defense      Programmed grooming

ANIMALS that live in environments that expose them to external and internal parasites have an array of behavioral defenses that may prevent, remove, or destroy such fitness-compromising parasites (3–5). Various aspects of foraging, microhabitat seeking, grouping, maternal, sexual, and social behavior patterns fall into this category. Grooming is a commonly performed behavior among rodents, felids, ruminants, and primates, which appears to function to remove ectoparasites. The frequency with which this behavior occurs has been revealed in several studies. For example, one-third of the waking time of laboratory rats may be spent in grooming (2), and in African antelope 80–200 oral grooming

bouts, consisting of 600–2,000 grooming episodes, are typically delivered per 12-h day (7). Although oral grooming undoubtedly functions in conditioning the hair coat by removing dirt and excessive oil, it has long been believed that an important function of grooming is ectoparasite removal (21).

Probably the best evidence for the effectiveness of oral grooming in removing ectoparasites comes from manipulations in which grooming is restricted or prevented. In mice, Murray (20) showed that average louse infestation increased more than 60-fold above baseline following interference with oral grooming using an Elizabethan collar. There have been no appropriately con-

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trolled systematic experiments on mammalian taxa other than rodents that have statistically documented the effectiveness of grooming in controlling ectoparasites. Some information is available from observations on individual cattle in which oral grooming was prevented with a harness. Following infestation with larval stages of the one-host tick *Boophilus microplus*, application of a harness resulted in increased tick infestation averaging between 5- and 10-times that of baseline (1,27). Also, data from individual cows showed that prevention of grooming allowed average louse numbers to increase up to about 15-fold over baseline (9). Cattle groom with their tongues, but other ungulates, including antelope and cervids, orally groom with the lateral side of the lower incisors and canines in upward scraping motions (7). Impala (*Aepyceros melampus*) are medium-sized antelope that typically inhabit open woodland areas that are often heavily infested with ticks (14). In impala and other small- or medium-sized antelope of Africa the lateral incisors and canine teeth comprise what has been referred to as the lateral dental grooming apparatus, which seems to serve no function in grazing or browsing but is well adapted for combing through the pelage and removing ectoparasites (11,13).

A model for the biological control of oral grooming, at least for animals continuously exposed to ectoparasites in nature, is a type of programmed grooming such that most grooming bouts are periodically activated independent of cutaneous stimulation (7). Thus, assuming grooming removes ectoparasites such as ticks, ectoparasites would be removed before they attach and begin to feed, and even before they cause cutaneous stimulation. The rate of such programmed grooming, perhaps loosely regulated by a grooming clock, is species-specific and would balance the costs of engaging in grooming against the benefits of ectoparasite removal and body maintenance for a particular species. The costs of grooming that have been identified include loss of water from saliva used in oral grooming (26), distraction from vigilance over predators (18), distraction in males from vigilance over females (7,17), and wear on the incisor-canine complex used in grooming (11). Although diseases can be transmitted by ectoparasites, the major cost of ectoparasites to native species can largely be attributed to blood removal (3).

With regard to determinants of grooming in antelope, we have previously conducted studies on the influence of body size (7), gender (7,17), dominance status (7,16), developmental phase (15), relatedness, age, and association (16), species-specific habitat (8), and changing levels of ticks in the environment (14). The purpose of Experiment 1 was to conduct an experiment on impala to test the actual effectiveness of oral self-grooming (or simply, oral grooming) in removing ticks, which was an assumed but untested function of grooming in the above studies. Captive impala were restrained from oral grooming by the use of neck harnesses, which allowed them to freely move about, eat, and drink, but largely prevented oral grooming of the shoulder and trunk. The animals could still scratch groom with the hindleg hooves and allogroom with herdmates. The subjects were exposed to larval stages of the one-host tick *Boophilus decoloratus*, which were applied by driving the animals into a tick-seeding corral.

If grooming is effective in removing ticks, then it would be adaptive for grooming to increase when the animals are exposed to increased numbers of ticks (14), which could be detected by an increase in tick-bite-associated stimuli. Systemically absorbed tick saliva or locally produced histamine could, theoretically, accelerate a central grooming clock. Experiment 2 was designed to examine the effects of experimentally exposing impala to larval *B. decoloratus* ticks by observing changes in rates of oral grooming, scratch grooming, and allogrooming.

## EXPERIMENT 1

This experiment tested the effects of disruption of oral grooming on the removal of ticks by comparing female impala wearing restraint neck harnesses that restricted oral grooming with female impala wearing control harnesses that allowed grooming.

### Method

*Study site and subjects.* The study was conducted September–October 1994 at a game farm in Transvaal, South Africa (25°00' S, 27°35' E). The impala were kept in a 1 ha enclosure surrounded by a 2.5 m high perimeter game fence (to which plastic boma sheeting was attached on one side) subdivided into three equal corrals with plastic boma sheeting. The enclosure was planted with fresh lucerne (alfalfa, *Medicago sativa*) upon which the impala readily grazed, supplemented with dry lucerne and nutritionally balanced antelope cubes. At one end was a 2.5 × 7 m capture area and adjacent to the capture area was a 5 × 27.5 m enclosure containing high swards of grass for use in tick seeding. The subjects were 11 adult female impala, free ranging prior to the experiment but accustomed to the presence of humans. All animals were individually identifiable by means of ear tags.

*Immobilization of impala, application of neck harnesses, and tick counting.* To capture impala for manipulations, the animals were herded into the capture area where they were subsequently immobilized by darting using a mixture of 15 mg fentanyl and 50 mg azaperone per impala, with 50 mg nalorphine antagonist used to reverse the fentanyl. Darting was accomplished with the Paxarms integrated sighting system in which dart velocity is adjusted along with trajectory so that the impact momentum of the dart remains constant regardless of distance. About 15 min following darting the impala were captured and placed on their sternums, the eyes covered, and the ears blocked with cotton (12). Prior to reversal with nalorphine and release, each impala was treated with a systemic antibiotic.

Neck harnesses, which were applied while the impala were immobilized, were constructed from 20 mm diameter plastic PVC piping (Fig. 1). The restraint harnesses (long harnesses) were tapered from shorter (24 cm) to longer (33 cm) lengths corresponding to the lengths of the dorsal and ventral lines of the neck. These long harnesses prevented much oral grooming while still allowing the animals to move about and feed and drink normally. Control harnesses (short harnesses) were of uniform 11 cm lengths and did not hinder oral grooming, but presumably provided a tactile effect similar to the restraint harnesses.

Measures of relative tick burden on immobilized impala were obtained using a patch-sampling method whereby all adult and nymphal ticks were removed from parts of the body where prior observations indicated most ticks were found. Accordingly, the head, neck (posterior from the head to the cranial edge of the scapula), chest (sternal area between the forelegs), and perianal region (4 cm out from the midline under the tail) of both sides, and the ear and foreleg (from the shoulder joint) of one side, were sampled using forceps and a flea comb according to the method previously described (14,17). If other body areas harbored ticks, this was noted. All ticks were later counted and identified under a dissecting microscope. In a separate study, patch sampling of ticks was positively and highly correlated with total tick counts on the same animals obtained by the digestion method, which provides counts of all ticks on an animal (19).

*Behavioral observations.* Behavioral observations were conducted from an elevated tower using a 15–60 × spotting telescope to observe impala at a distance of 50–150 m. Focal animal samples of 20 min were employed to record grooming behavior

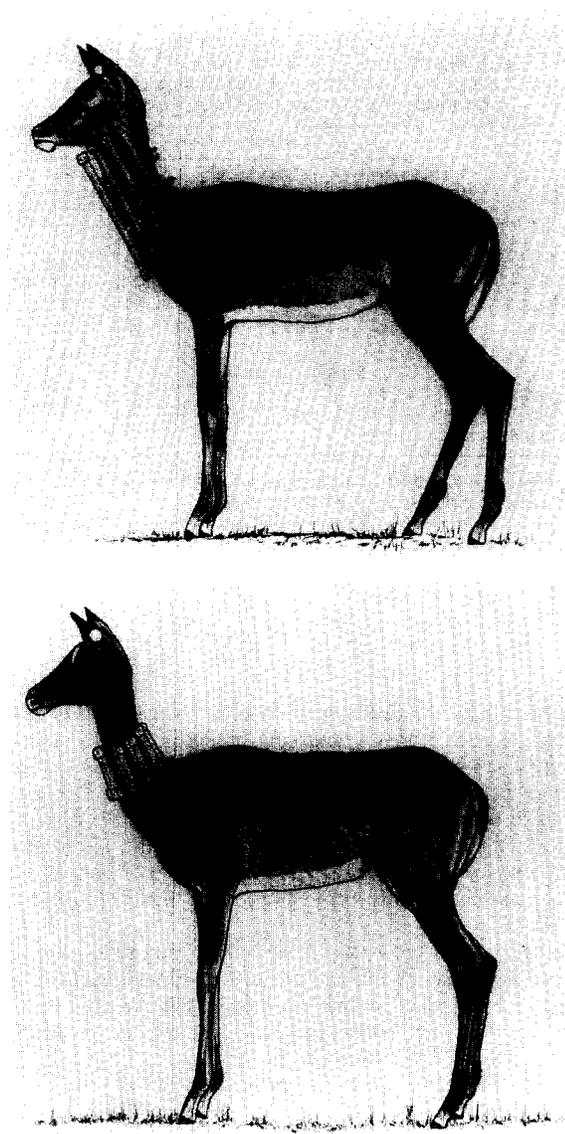


FIG. 1. Top: drawing taken from a photograph illustrating the restraint harness that prevented oral grooming of the anterior part of the body but still allowed the impala to freely move about, eat, and drink. Bottom: drawing taken from a photograph of the control harness that did not interfere with grooming but provided tactile stimulation on the neck similar to that of the restraint harnesses (drawings by Emma Mooring).

onto a Tandy 102 laptop computer. Observations were made only when focal animals were standing, as the impala rarely groomed when lying down. (Pilot observations indicated that harnesses did not change time spent lying down; thus, focal observations were a reliable sample of total time spent grooming.) Grooming rates were later extrapolated to bouts and episodes per hour. The experiment involved a total of 101 h of focal observation.

During oral grooming, each head movement (denoting a single scrape with the lateral incisors) was recorded as a grooming episode, with a connected series of episodes constituting a grooming bout. Oral grooming bouts are typically directed to one body site, and we recorded the body region and side of the body groomed. Scratch grooming bouts, consisting of episodes of scratches with the hind hooves, are typically directed to one site

on the head or neck. Scratch grooming episodes and bouts were recorded in the same manner as oral grooming. Adult impala engage in a unique form of highly reciprocal allogrooming (6,15) that is always directed to the head and neck of the grooming partner. Allogrooming bouts and episodes received and delivered in an encounter were recorded along with noting the identity of the partner. Typically, 10–12 bouts of oral grooming with the lateral incisors are exchanged during an encounter. Although both bouts and episodes of grooming were tabulated, data are presented only for episodes because analyses gave the same significant results for both bouts and episodes, and episodes delivered portray the actual amount of grooming received. Impala allogrooming is very symmetrical, with bouts or episodes delivered and received being highly correlated (6,15). Thus, we used only allogrooming delivered in the data analysis and, as in self-grooming, we report only grooming episodes.

*Experimental design.* We predicted that impala restrained from oral grooming with long harnesses and subsequently seeded with ticks would carry higher tick loads than control animals, and that following the removal of the harnesses there might be a catch-up increase in oral grooming that would not occur in the control group because their short harnesses did not restrict grooming. The experiment was designed to test these predictions.

At the beginning of the experiment, during immobilization, five female impala were fitted with restraint harnesses and six females with control harnesses. The experiment was conducted during the low-tick season (hot-dry season), when we did not expect naturally occurring ticks to be present in the enclosure. However, in the initial immobilization all subjects were patch sampled to confirm that they were not carrying ticks. They were then left undisturbed for a 10-day habituation period during which one 20-min focal observation per impala was conducted each day. At the end of habituation impala were herded into the tick seeding enclosure, into which approximately 110,000 larval *B. decoloratus* ticks, representing an estimated 10,000 larvae per impala, had been distributed on the tops of swards of grass. The impala were kept there quietly for 1 h and periodically encouraged to move around through the grass to increase tick exposure. Following release from this enclosure, search for remaining larvae on the grass confirmed that most ticks had attached to the impala or fell off the tops of grass. Each impala was then observed daily in 20-min focal observations for the next 2 weeks.

During week 3 following tick seeding, when it was estimated that most female ticks had reached the adult stage and had started to engorge, the impala were again immobilized, the harnesses removed, and each animal patch sampled for ticks. Not all ticks mature at the same rate; when most will have just reached the adult stage, some ticks will still be immature while others will have engorged and dropped off. Male ticks imbibe only a little blood before mating with females and dropping off, and patch sampling during week 3 was not considered to be a reliable time to estimate adult male tick numbers. Nymphal ticks (either male or female) are much smaller than adults and presumably more difficult to remove by grooming. Although all ticks found were counted, attention was focused primarily upon adult female ticks, both engorged or nonengorged. This is the stage and sex that is most costly in removing blood; males and nymphs extract relatively little blood. Following patch sampling, postharness 20-min observations were conducted daily over the next 5 days.

*Data analysis.* Results for tick load are reported as group medians for adult female ticks (nonengorged and engorged) and for all stages and sexes of ticks combined. Results for grooming are reported as group medians of individual means during the tick-seeded and postharness phases. Statistical analysis involved pair-wise comparisons using the nonparametric Wilcoxon

signed-ranks test for changes in grooming behavior within groups, and the Mann-Whitney test for independent samples for comparisons between groups in grooming and tick load (25). Because we had made specific a priori predictions about the direction of differences in tick numbers and grooming between restrained and control impala, the statistical tests for these measures were one tailed (10), with the level of significance set at  $p < 0.05$ .

### Results

**Comparison of tick load.** Impala in both groups that were patch sampled for relative tick load harbored many fewer ticks than the 10,000 adult ticks representing an individual animal's proportion of ticks from the seeding enclosure. Following exposure of the impala to the larval ticks, undoubtedly most of the larvae were knocked off the grass and fell to the ground, fell off the impala, or were groomed off, as would happen in nature. The only other tick species found on the impala, *Rhipicephalus evertsi*, was found in such low numbers (mean 0.6 per subject) that they are disregarded for the sake of the experiment (*R. evertsi* migrate to the perianal area and did not differ between groups).

Differences between the control and restrained impala in numbers of female ticks and of all ticks, shown in Fig. 2, were rather dramatic and significant ( $p < 0.003$ ). Patch sampling of the control impala during week 3 following tick exposure revealed a median of only 2.5 female ticks and 16 ticks of all stages per impala. Restrained impala carried 20 times as many female ticks (median 49) and 9 times as many ticks overall (median 141) as control impala. In both control and restrained impala, visual inspection of parts of the body not specifically sampled revealed very few ticks and no evident difference between control and restrained impala.

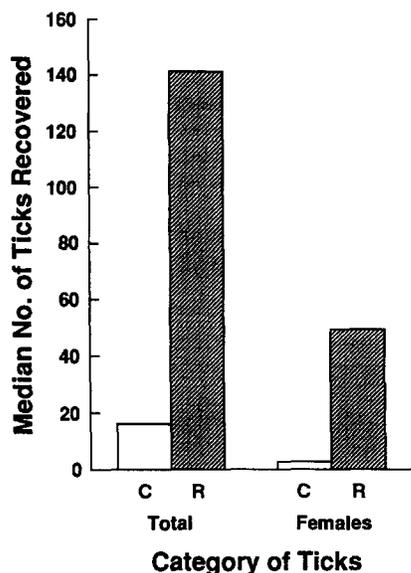


FIG. 2. Number of ticks recovered by patch sampling of control (C: open bars) and restrained (R: crosshatched bars) impala in the third week following tick seeding. Shown are median number of ticks of all stages (i.e., adult females, adult males, and nymphal ticks) and adult female ticks that are unengorged or engorging. Differences between the restrained and control impala for both comparisons were highly significant ( $p < 0.003$ , Mann-Whitney test).

TABLE 1  
PERCENTAGE OF ORAL AND SCRATCH SELF-GROOMING BOUTS DELIVERED TO VARIOUS BODY REGIONS BY CONTROL AND RESTRAINED IMPALA DURING DIFFERENT STAGES OF THE EXPERIMENT

Body Region	Experimental Phase					
	Habituation		Tick-Seeded		Postharness	
	Control	Restrained	Control	Restrained	Control	Restrained
Oral Grooming						
Shoulder	20	0*	18	8	13	30*
Trunk	30	10*	26	15	25	34
Rump	22	78*	27	46*	44	22
Legs	28	12	30	32	19	15
Scratch Grooming						
Head	87	80	56	28	46	57
Neck	13	6	44	54	54	38
Shoulder	0	13*	0	18*	0	5

\* Indicates a significant difference ( $p < 0.05$ ) between control and restrained impala by the Mann-Whitney test.

Key: shoulder = shoulder and chest; trunk = flank, back, and belly; rump = rump and tail.

Percentages in columns do not always equal 100% due to rounding.

In examining the distribution of ticks on the body of control impala, the neck, foreleg, and ears harbored 30, 26, and 39%, respectively, whereas in the restrained impala the neck, foreleg, and ears harbored 72, 21, and 6%, respectively. The ears of animals in both groups actually contained almost the same mean number of ticks (about five ticks per ear) as did the heads and tails (2–5% of ticks), but the neck and foreleg of the restrained impala harbored significantly more ticks than control impala ( $p < 0.01$ ).

**Comparison of grooming.** The restraint harnesses altered the distribution (Table 1) and amount of oral grooming. During the habituation, restrained impala seemed not to be able to orally groom the shoulder, which received 20% of oral grooming in controls ( $p < 0.02$ ). However, by the time of the tick-seeded phase, the restrained impala managed to deliver 8% of oral grooming episodes to the shoulder (compared with 18% by controls). As a function of the harness restricting oral grooming to the shoulder, the restrained impala appeared to partially compensate by scratch grooming to the shoulder (13 and 18% of scratch-grooming episodes during habituation and tick-seeded phases, respectively), whereas control impala delivered no scratch grooming to the shoulder ( $p < 0.04$ ). Exposure to ticks increased oral grooming in the control impala from a median of 115 to 189 episodes per hour ( $p < 0.02$ ), and in restrained impala from 16 to 38 episodes per hour ( $p < 0.03$ ). Allogrooming rate also increased in both control and restrained impala following tick-seeding ( $p < 0.03$ ), but there was no significant change in scratch grooming. When both groups of impala were pooled ( $n = 11$ ), the increase in oral grooming and allogrooming episodes following tick seeding was highly significant ( $p < 0.001$ ), and scratch grooming also reached significance ( $p < 0.05$ ). Spearman rank order correlation showed a significant negative correlation between oral grooming rate during the tick-seeded phase and total number of ticks recovered from impala ( $r_s = -0.72$ ,  $p < 0.01$ , one tailed), indicating that impala that groomed the most had the fewest ticks.

As expected, while wearing harnesses the total amount of oral grooming differed markedly between the control and restrained impala (Fig. 3). During the tick-seeded phase, restrained impala

delivered one-third the amount of oral grooming to their bodies as control impala ( $p < 0.003$ ). Following removal of the harnesses, there was a major increase in oral grooming in previously restrained impala from a median of 44 to a median of 455 episodes per hour ( $p < 0.03$ ); no increase occurred in the control impala. The previously restrained impala, which oral groomed 10 times more in the postharness phase than they did in the tick-seeded phase, were also grooming 2.5 times more than control impala during the postharness phase ( $p < 0.003$ ). The previously restrained impala directed a higher percent of oral grooming to the shoulder ( $p < 0.03$ ) and trunk (which they could now easily reach), while reducing grooming of the rump (Table 1). Neither scratch grooming nor allogrooming changed significantly in either group following the removal of harnesses (Fig. 3).

#### EXPERIMENT 2

Oral grooming increased in impala of Experiment 1 after the impala (habituated to harnesses) were exposed to ticks. Experiment 2 more explicitly analyzed changes in grooming rates when unrestrained, freely moving impala were subjected to about the same number of larval ticks in the tick-seeding corral as in Experiment 1. Grooming rates were recorded prior to tick expo-

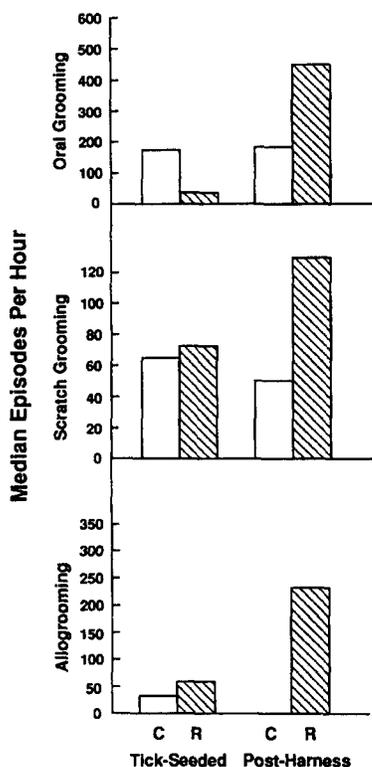


FIG. 3. Rates of grooming behavior extrapolated to grooming episodes per hour delivered by control (C: open bars) and restrained (R: cross-hatched bars) impala during the tick-seeded and postharness phases of Experiment 1. The data are expressed as medians of individual means. Oral self-grooming did not change after removal of the harnesses in control impala but increased markedly and significantly in previously restrained impala ( $p < 0.03$ , Wilcoxon test) and differed significantly from the control group in the postharness phase ( $p < 0.003$ , Mann-Whitney test). Scratch grooming and allogrooming did not change significantly in either group between the two phases.

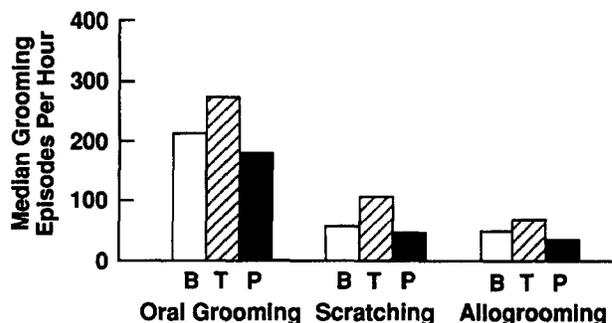


FIG. 4. Grooming behavior of adult female impala in Experiment 2 during: baseline (B: open bars), prior to seeding with ticks; following tick seeding (T: crosshatched bars); and post-tick phase (P: solid bars) following removal of ticks by acaricide. The data are expressed as medians of individual means. There was a significant increase in oral and scratch self-grooming in the tick-seeded phase compared with baseline ( $p < 0.04$ , Wilcoxon test) and a significant decrease in oral and scratch self-grooming in the post-tick phase ( $p < 0.001$ , Wilcoxon test).

sure, after tick exposure in the tick-seeding corral, and after tick removal with an acaricide.

#### Method

The subjects were 15 female impala, including impala of Experiment 1, all of which were free-ranging prior to the experiment and accustomed to the presence of humans. The study site was the same as in Experiment 1, as were the methods of immobilization and recording behavior. The impala were observed June–August 1994 during three phases, each of which was 3 weeks in duration: 1) baseline, prior to tick seeding, 2) following exposure to around 9000 larval *B. decoloratus* ticks per animal, and 3) beginning 1 week after treatment with an acaricide (Drastic Deadline, Bayer SA), by which time all ticks had died and dropped off the animals. The corrals where impala were kept had been treated (Bayticol, Bayer SA) to remove ticks following acaricide treatment of the impala. Individual means for grooming were obtained from three 20-min observations on each animal per week, for a total of 154 observation hours. Data are presented as group medians of individual means for grooming episodes, as in Experiment 1. Because specific a priori predictions were made regarding the direction of grooming following tick exposure and tick removal, the statistical analyses were by one-tailed Wilcoxon matched-pair signed rank tests (10,25), with the level of significance set at  $p < 0.05$ .

#### Results

Grooming rates, expressed as median episodes per hour, indicated that oral grooming and scratch grooming increased following tick exposure and declined following removal of ticks (Fig. 4). The increase in oral and scratch grooming following exposure to ticks, while moderate, was consistent and significant ( $p < 0.04$ ). Interestingly, the proportion of oral grooming delivered by impala to the legs (where tick larvae initially alight upon a host) increased from 18% during baseline to 63% immediately following tick seeding on the same day. The decrease in oral and scratch grooming following removal of ticks with the acaricide was substantial and highly significant ( $p < 0.001$ ). Allogrooming episodes increased only slightly, and not significantly, following tick seeding, but declined significantly after tick removal ( $p > 0.03$ ).

## GENERAL DISCUSSION

Experiment 1, which involved interference with but not complete prevention of oral grooming, resulted in the restrained impala harboring 20 times as many female adult ticks as in the control situation. The animals could still groom the posterior regions of the body and could still scratch the head and shoulder, as well as engage in allogrooming. Allogrooming commonly occurs among adult female impala (6,14), and one would predict that allogrooming, in which scrapes with the lower incisor-canine complex are delivered in the same manner as in oral self-grooming (6,15), would also be effective in removing ticks. Scratch grooming, as well, undoubtedly has some effect in dislodging ticks from the head and ears. Thus, all three forms of grooming taken together would have an even greater impact in controlling ticks than that represented by the 20-fold difference in tick loads between restrained and control impala reported here.

Most ticks on the previously restrained impala were on the neck. In oral grooming, impala scrape the lateral incisors through the pelage in a combing movement. In unrestrained impala, grooming the shoulder, trunk, and legs probably removed ticks as they moved anteriorly through the pelage before starting to attach and feed. Thus, in the restrained impala more ticks would have survived to move onto the neck, and the neck harness would have largely blocked scratch grooming and allogrooming from dislodging ticks from that area.

Following immobilization in week 3 after tick seeding, the harnesses were removed and most of the remaining ticks collected for counting. In the ensuing 5 days the control impala did not change in grooming rate but the restrained impala increased their grooming to a level of 2.5 times the rate of controls. As mentioned in the introduction, we have postulated that the periodic occurrence of bouts of grooming may be regulated by an internal timing mechanism, which may be modulated to run at a higher rate by systemic stimuli associated with tick bites, such as tick saliva (7,14). The postharness increase in grooming in the previously restrained impala may reflect a reaction to the aftereffects of tick feeding such as residual, systemically absorbed tick saliva, and/or a behaviorally driven catch-up of grooming from deprivation of oral grooming. A distinction between tick-related grooming and catch-up grooming could be resolved by conducting an additional experiment with animals that are fitted with restraint collars but not seeded with ticks. The results of Experiment 2 (discussed below) are consistent with the tick-induced acceleration of grooming.

How the finding on the rather dramatic role that grooming plays in controlling ticks may relate to the fitness of antelope and other ungulates in nature is estimated by examining the costs of ticks in terms of extraction of body resources. These costs have been explored in livestock because of economic concerns. In growing calves, a single engorging female tick produces a growth decrement of 0.6–10.0 g, depending upon the tick species, amounting to an annualized loss in weight gain of up to 3.1 kg per engorging tick per year (14,17,22,23). Other studies on the costs of ectoparasites are reviewed elsewhere (3). Given the amount of body resources that may be consumed by engorging female ticks, the 20-fold difference in tick numbers between the animals with impaired grooming vs. the control situation could translate into important costs in fitness when body resources are in high demand, such as in males competing for a territory and acquiring females, or females when lactating and rearing young.

The established effectiveness of grooming in removing ticks points to the usefulness of the programmed grooming model in integrating a balance between the costs of engorging ticks and the costs of grooming. One cost of grooming is distraction from vigilance by territorial males over females, and territorial male antelope, including impala, groom less than half as much as female impala and even less than bachelor males on their own territories (7,17). In accordance with the programmed grooming model and the established link between grooming and removal of ticks, one study found that territorial males had more than six times as many ticks as female impala (17).

A prediction from the programmed grooming model, supported by the findings of the present study, relates to body size, grooming rate, and tick load. Antelope species of smaller body size, such as Thomson's gazelle, *Gazella thomsonii*, groom much more frequently than those of larger body size, such as wildebeest, *Connocheates gnu* (7). Correspondingly, Thomson's gazelle carried a much lower density of ticks on the body surface than wildebeest in the same environment (24). The negative correlation found in Experiment 1 between grooming rate and tick load after tick seeding is additional support of programmed grooming; those impala with the fewest ticks had groomed the most. The alternative model of stimulus-driven grooming would have predicted the opposite: those impala with the fewest ticks would have groomed the least. Of course, centrally mediated programmed grooming (perhaps modulated by tick saliva) and stimulus-driven grooming as the result of cutaneous irritation once the tick attaches and begins to feed (28,29) would be expected to operate concurrently, with tick-induced grooming in response to irritation being performed on top of periodic preventive grooming regulated by a grooming clock independent of cutaneous irritation.

The increase in grooming as a function of exposure to ticks, seen in Experiment 1 and addressed explicitly in Experiment 2, is consistent with the hypothesis that some systemically absorbed substance may modulate grooming to occur at a higher rate. This finding also supports the concept that the higher rate of oral grooming in three species of antelope in Kenya (impala, Thomson's gazelle, and wildebeest) than at the tick-free San Diego Wild Animal Park (7) was due to exposure to ticks in Kenya but not at the SDWAP. The findings are also relevant to a study of grooming in impala across seasons in Zimbabwe. When adult ticks were abundant (warm-wet season), grooming was more frequent than when only larval ticks were present (14). The present study confirms that this difference was due to the attachment and feeding of ticks.

Taken together, the two experiments demonstrate that oral grooming is very effective and important in removing ticks in free-ranging impala. Correspondingly, exposure to ticks, and subsequent infestation by ticks, increases the rate of grooming.

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