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Interactions between impala and oxpeckers at Matobo National Park, Zimbabwe

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Summary

In order to better understand the symbiotic relationship of the oxpecker–mammal association and the role that oxpeckers play in controlling their hosts' tick burdens, interactions between yellow-billed oxpeckers (*Buphagus africanus*) and impala (*Aepyceros melampus*) were investigated at Matobo National Park, Zimbabwe during the wet and dry seasons. Oxpeckers devoted 30–35% of attendance time to foraging upon impala hosts. The ears were preferred for foraging above all other body regions, and foraging sessions directed to the ears were longer than sessions on other areas, apparently due to high tick infestation on host ears. Two-thirds of adult ticks (mostly the blue tick *Boophilus decoloratus*) collected from impala females were from the ears, and heavy infestations of immature ticks on the ears were common. The majority of oxpecker foraging (71–74%) was directed to the ear, head, and neck area where impala are unable to self-oral groom. Most adult ticks (75–77%) were found on the ears, head, and neck of sampled impala, indicating that oxpeckers foraged so as to maximize adult tick intake. Adult tick abundance in the vegetation, and presumably on impala, was much greater in the wet season than in the dry season. Oxpeckers spent significantly less time foraging upon impala in the wet season compared with the dry season, reflecting the presumed greater abundance of adult ticks on hosts during this time. Impala hosts tolerated oxpeckers 86% of the time, and 42% of oxpecker-tolerant impala accommodated foraging activity by lowering an ear, inclining the head, or standing still. An interaction was apparent between the tick-removal strategies of oxpeckers and their impala hosts in that impala reduced their grooming rate when oxpeckers foraged upon them to 11–36% of their grooming rate in the absence of oxpeckers, thereby reducing the cost of tick control.

Key words: foraging, grooming, impala, oxpeckers, symbiosis, ticks

Résumé

Pour mieux comprendre la relation symbiotique de l'association pique-boeufs-mammifères et le rôle que jouent les pique-boeufs dans le contrôle des tiques de leurs hôtes, on a analysé les interactions entre les pique-boeufs à bec jaune

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(*Buphagus africanus*) et les impalas (*Aepyceros melampus*) au Parc National de Matobo, au Zimbabwe, en saison sèche et en saison des pluies. Les pique-boeufs consacraient de 30 à 35% de leur temps d'attention à se nourrir sur des impalas. Ils préféraient les oreilles à toute autre partie du corps et le temps consacré à se nourrir sur les oreilles était plus long que sur toute autre partie du corps, ceci étant dû semble-t-il à un plus haut degré d'infestation des oreilles des hôtes par les tiques. Les deux tiers des tiques adultes (surtout la tique bleue *Boophilus decoloratus*) recoltées sur les impalas femelles provenaient des oreilles, et de fortes infestations des oreilles par des tiques immatures sont communes. La plus grande part des recherches de pique-boeufs (71 à 74%) se faisait au niveau des oreilles, de la tête et du cou, là où les impalas sont incapables de se toiletter eux-mêmes. On trouvait la plupart des tiques adultes (75 à 77%) sur les oreilles, la tête et le cou des animaux analysés, ce qui indique que les pique-boeufs se nourrissaient à ces endroits pour maximaliser la prise de tiques adultes. L'abondance de tiques adultes dans la végétation, et probablement sur les impalas, était bien plus grande pendant la saison des pluies que pendant la saison sèche. Les pique-boeufs passaient significativement moins de temps à se nourrir sur les impalas en saison des pluies qu'en saison sèche, ce qui reflétait l'abondance probablement plus grande de tiques adultes sur leurs hôtes pendant cette saison. Les impalas hôtes toléraient la présence des pique-boeufs 86% du temps, et 42% des impalas consentants facilitaient l'activité de nourrissage en abaissant l'oreille, en baissant la tête ou en restant tranquilles. Il semblait donc exister une interaction entre les stratégies des pique-boeufs pour enlever les tiques et les impalas hôtes, en ceci que les impalas réduisaient leur temps de toilettage jusqu' à 64 à 89% de ce qu'il aurait été en l'absence de pique-boeufs, ce qui réduit d'autant le coût du contrôle des tiques.

Introduction

The association between oxpeckers (*Buphagus* spp.) and their mammalian hosts in Africa is well known, and recent evidence indicates that this relationship may be among the best examples of symbiosis between terrestrial vertebrates (Breitwisch, 1992). Current evidence points to fitness benefits from the association for both oxpecker and host. By removing ticks, oxpeckers gain the major food item in their diet (Attwell, 1966; Bezuidenhout & Stutterheim, 1980), and hosts are helped in controlling tick infestations that may lead to mortality or morbidity (Lightfoot & Norval, 1981; Norval *et al.*, 1988; Hart, 1990). One would therefore expect to see oxpeckers foraging so as to optimize tick intake, and hosts tolerating or accommodating oxpecker foraging when threatened by ticks. Previous studies have tended to examine oxpecker biology and host selection in isolation from the host animal and have not taken into consideration the interaction that takes place in a symbiotic relationship.

A prime factor influencing oxpecker foraging behaviour would be tick abundance, which varies seasonally and affects the tick burdens on host animals (Mulilo, 1985; Kaiser, Sutherst & Bourne, 1991). For example, oxpeckers should be able to forage more quickly and efficiently during the wet season, when environmental tick challenge and host tick loads are typically greatest (Mooring, Mazhowu & Scott, 1994), than during the dry season, when they may have to spend more time foraging for sparsely distributed ticks on hosts. Host factors such as habitat preference, body mass, group size, and hair length may interact to make a host more or less attractive to oxpeckers by influencing host tick burden and oxpecker foraging efficiency. Host response to oxpeckers would also play a role in host selection. There are two ways that a potential host can respond to an oxpecker that attempts to land and forage: it can reject the oxpecker, for example by swinging the head or jumping, or it can tolerate its presence. Toleration can be expressed either by the host acting indifferently, or by the host accommodating the bird's foraging efforts by making certain body regions accessible (such as by lifting the tail or lowering the ears) or by standing still during foraging sessions. Typical host response probably plays an important role in which host species oxpeckers learn to prefer or avoid.

In controlled experiments with cattle, oxpeckers removed 95·7–99·9% of adult ticks and 21–90% of larvae and nymphs (Bezuidenhout & Stutterheim, 1980). While oxpeckers are presumably as effective in removing ticks from wild hosts, it must be remembered that some wild hosts have their own behavioural strategies for controlling ticks. Impala (*Aepyceros melampus* Licht.) exhibit well-developed self-grooming behaviour (Hart *et al.*, 1992) as well as a unique form of reciprocal allogrooming (Hart & Hart, 1992; Mooring & Hart, 1992a, 1993) that appears to function primarily to remove ticks before they can attach and engorge. In Zimbabwe, tick challenge was the primary determinant of impala grooming rate (Mooring, 1995), and territorial males that engaged in reduced grooming during the breeding season harboured more ticks than females (Mooring & Hart, 1995). Impala are unusual in being the smallest antelope regularly attended by oxpeckers, suggesting that impala may harbour more ticks than comparably-sized antelope that are not attended (Hart, Hart & Mooring, 1990). Grooming, as well as toleration or accommodation of oxpeckers, may be behavioural strategies used by impala to cope with increased exposure to ticks in their brushy ecotone habitat. If both impala grooming and oxpecker foraging function to remove ticks, one might expect an interaction effect whereby impala with access to oxpeckers reduce their grooming in order to reduce the cost of tick control.

Investigation into these questions is important not only for better understanding of the biology of the oxpecker–mammal symbiosis, but also for improved conservation and management of wildlife populations. Serious tick problems exist in many national parks and game farms in Africa where limited area, overstocking, and historical events have allowed excessive buildup of tick populations (Norval & Lightfoot, 1982). One promising management approach for the control of ticks is the introduction of oxpeckers to problem areas in order to naturally regulate tick burdens on wild hosts (Mundy, 1983; White, 1990; Cole, 1992). Little field research has attempted to assess the effectiveness of oxpeckers in controlling ticks on wild animals, and information of this sort can contribute to the successful use of oxpeckers as management tools.

The purpose of this study was to investigate the effect of tick challenge upon the foraging behaviour of oxpeckers, and the response of impala to oxpecker foraging. The study involved observations of oxpecker foraging, impala grooming, and typical impala response to oxpeckers during two seasons of the year in which tick challenge differed. In order to assess tick challenge, both vegetational sampling and sampling of impala tick loads were undertaken.

Materials and methods

Study site

The study was conducted within the Whovi Wilderness Area (game park) of Matobo National Park (20°30′S, 28°30′E). Matobo has been the site of several previous studies of oxpecker biology and host preference (Dale, 1992a, b; Grobler, 1976, 1979; Grobler & Charsley, 1978; P. J. Mundy, unpubl. data). Field work was carried out from 20 October to 26 November 1992, and from 3 March to 10 April 1993, periods that corresponded to the late hot-dry (dry) season and late warm-wet (wet) season, respectively. Yellow-billed oxpeckers (*B. africanus* L.) at Matobo were descended from 47 birds re-introduced to the game park in 1975 (Grobler, 1976). The population flourished and in 1990 were estimated to number around 200 birds (Dale, 1992a). A small population of red-billed oxpeckers (*B. erythrorhynchus* Stanley) also exists at Matobo, representing 1–4% of the total oxpecker population (unpubl. data). Observations were focused primarily upon the yellow-billed oxpecker.

Vegetational tick sampling

Vegetational sampling for ticks was performed by drag and removal plot sampling. Drag sampling captured receptive ticks of all life stages, adults and immatures, while removal plots captured adult ticks only, both receptive and quiescent. All sampling was done in the vicinity of Mpopoma Dam in areas frequented by impala. Four drag sites were sampled per week, two each in grassland and open woodland, with two 50 m replicates dragged per site. Four 10 m × 10 m removal plots were sampled, two per week, in grassland and open woodland habitats. Ticks were stored in 70% alcohol and later counted and identified at the Tick Research Unit, Veterinary Research Laboratory, Harare. Further details of the sampling methods are given in Mooring (1995) and Mooring *et al.* (1994).

Sampling impala tick burden

Taking advantage of a population reduction exercise performed by the Department of National Parks in November 1992, it was possible to sample 8 female and 11 male adult impala. Estimates of relative tick burden were obtained by using a patch sampling method whereby all adult ticks were removed from the ears, face, neck, and foreleg on one side of the midline, and the perianal region, according to the method described by Mooring & Hart (1995). All ticks were later identified by the Tick Research Unit, Veterinary Research Laboratory, Harare.

Observations of oxpeckers and impala

Observations were focused primarily upon the yellow-billed oxpecker, with the red-billed variety only rarely observed. Behavioural observations of oxpeckers in the presence of impala were conducted at Mpopoma Dam using a 15–60 x telescope and recording into a portable computer. Focal oxpecker observations and scan sampling methods (Altmann, 1974) were employed to record foraging and other attending behaviours. A total of 99 focal sessions comprising 28·4 h of observations were completed.

Oxpecker 'attendance' of an impala host referred to the total time that oxpeckers spent upon a particular animal. Attending oxpeckers could engage in a variety of behaviours, the most typical ones being perching and foraging by means of the scissoring or plucking techniques (see Bezuidenhout & Stutterheim, 1980, for a full description of behaviours). Foraging technique, host body region foraging was directed to, the amount of time spent actively foraging on different body areas, and total attendance time were recorded during continuous observations, and activity budgets were calculated by scan sampling at 2-min intervals. Also recorded was the age class (adult or immature) and flock size of oxpeckers, and the impala herd size. Oxpecker ages were determined by bill colour according to Stutterheim, Mundy & Cook (1976).

When oxpeckers alighted upon an impala and attempted to forage, the response of the host (rejection, toleration, accommodation) was recorded. The proportion of impala that rejected oxpeckers' attempts to land and forage was recorded by counting overt responses by the host (swinging or shaking of the head, jumping, running away) as rejections; all cases of attendance of less than 10 s duration were omitted. An accommodation response was recorded when the impala lowered an ear, inclined its head, or stood still in response to oxpecker foraging. If the host initially tolerated the bird and allowed it to forage, and later rejected it, the host response was classified as toleration.

Host grooming behaviour was recorded when oxpeckers were attending impala. Impala oral groom by combing the pelage with their incisor-canine teeth and scratch groom with the hoof of the hindleg. Self-oral grooming is directed to all parts of the body except the head and neck, while allogrooming and scratching are directed to the head and neck area which the animal cannot reach by self-oral grooming. Each oral combing or scratching movement was recorded as an 'episode', with a connected series of episodes constituting a 'bout'. Data on the grooming behaviour of female impala when oxpeckers were absent was collected as part of another study conducted at the same site and during the same time frame, using the methods of this study; these data are cited from Mooring (1995).

Results

Vegetational tick sampling

To estimate tick density in the vegetation, 64 drag replicates and 16 removal plots were sampled in the dry and wet seasons in grassland and woodland habitat. No adult ticks were recovered from vegetational sampling during the dry season, while in the wet season an average of 1·0 adult tick per 50 m drag and 24 adult ticks per removal plot were collected (Mann–Whitney; drags: $Z=3{\cdot}6$, $P<0{\cdot}0003$; removal plots: $Z=3{\cdot}2$, $P<0{\cdot}001$). Of the adult ticks collected by drag samples, 90% were the brown ear-tick *Rhipicephalus appendiculatus* Neumann and 6% were the red-legged tick *R. evertsi* Neumann, while 72% of larvae were the blue tick *Boophilus decoloratus* (Koch). Removal plot sampling of adult ticks collected 97% *R. appendiculatus* and 3% *R. evertsi.*

Impala tick burden

The adult ticks collected from the nineteen culled adult impala (8 females, 11 males) that were patch-sampled for relative tick burden were *B. decoloratus*, 79%; *R. evertsi*, 14%; and *R. appendiculatus*, 6%. Of a total of 205 ticks removed from female impala, 67·3% were on the ears. The remainder of the ticks collected were distributed throughout the body (face, 5·9%; neck, 3·4%; foreleg, 16·1%; tail, 7·3%). There was no difference in the number of ticks removed from males, and the proportion of ticks infesting the combined ear, face, and neck area was very similar (females, 77%; males, 75%). Although immature ticks were not collected, it was noted that 9 of the 19 adults sampled (47%) had heavy to very heavy infestations of larval and nymphal ticks in the ears.

Observations of oxpeckers

Mean (± SE) oxpecker flock size per impala herd was 2·3 (± 0·2) in the dry season and 3·4 (± 0·3) in the wet season, ranging between 1 and 9 oxpeckers. The average number of oxpeckers attending a single impala was 1·5 (± 0·1) in both seasons, although as many as 6 oxpeckers were observed upon one impala at a time. The longest time of continual attendance on the same host was 26 min (dry season) and 20 min (wet season). The number of oxpeckers attending an impala herd was positively correlated with the size of the herd (Spearman: $r_s = 0{\cdot}88$, $Z = 2{\cdot}3$, $P < 0{\cdot}02$). Oxpecker flock size did not increase in the same proportion as the increase in impala herd size, however, as reflected in fewer oxpeckers per host animal in larger herds.

The foraging behaviour of oxpeckers typically seen on impala is depicted in Fig. 1, as well as a typical accommodation response of impala. The percentage of attempts by oxpeckers to land and forage upon impala that were tolerated (not rejected) by the host was 84% in the dry season and 89% in the wet season (not significantly different), or a mean of 86%. For those impala that tolerated oxpecker foraging activities, the percentage that accommodated oxpeckers by lowering an ear, inclining the head, or standing still to facilitate foraging efforts was 55% ($N = 161$) in the dry season and 20% ($N = 103$) in the wet season, or a mean of 42%. From the scan samples, the percentage of attendance time that oxpeckers devoted to foraging was 31% ($N = 609$) in the dry season and 29% ($N = 278$) in the wet season (not statistically different), which was a mean of 30%. Based on continuous time sampling of oxpeckers upon hosts, the percentage of attendance time devoted to foraging was 38% in the dry season and 33% in the wet season, or a mean of 35%. The percentage of time on a host that oxpeckers devoted to perching from scan samples was 49% and 55% for the dry and wet seasons, respectively, and did not differ between seasons.

The body areas of impala that were foraged upon by oxpeckers in the two seasons are displayed in order of decreasing preference in Fig. 2. The ears were the single most preferred foraging site, being utilized for up to 50% of foraging time. In addition, during the dry season oxpeckers spent more time per foraging session on the ears compared with all other areas (mean ± SE: ears = 35 ± 2 s, all other areas = 19 ± 1 s), which was highly significant (Wilcoxon: $Z = 6{\cdot}3$, $P < 0{\cdot}0001$). In the wet season, oxpecker sessions on the ears were also significantly longer ($Z = 2{\cdot}0$, $P < 0{\cdot}05$). The head (excluding the ears) was the next most

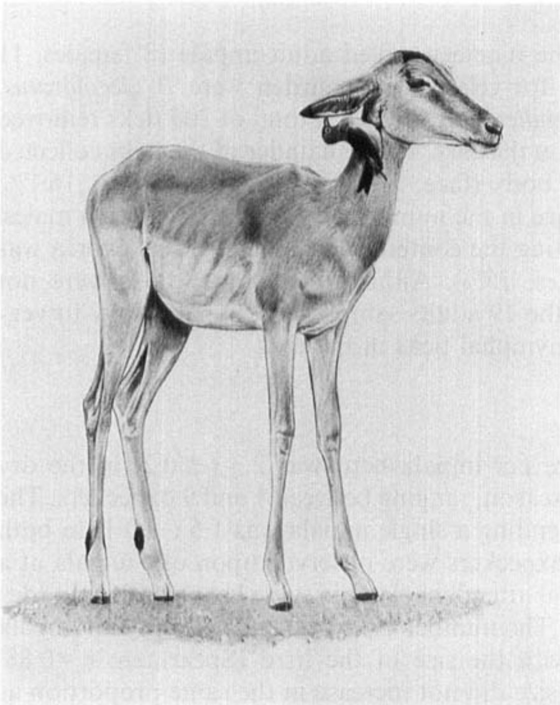

Fig. 1. Typical accommodation behaviour is demonstrated by a female impala lowering its ear in order to facilitate foraging by a red-billed oxpecker. Drawn by Emma Mooring from a photograph.

preferred body site after the ears, followed by the neck area. Oxpeckers concentrated their foraging efforts on the ears, head, and neck, accounting for 71% of oxpecker foraging in the dry season and 74% in the wet season.

The time that oxpeckers spent foraging per host was 72% longer in the dry season than in the wet season, with oxpeckers devoting a mean (± SE) of 1·65 (± 0·13) min foraging per host in the dry season compared with 0·96 (± 0·11) min during the wet season (Mann-Whitney: $Z=3{\cdot}6$, $P<0{\cdot}0004$). Because the percentage of attendance time spent foraging did not change between seasons (mean = 30–35%; see above), the time that oxpeckers spent attending impala was also greater in the dry season than in the wet season, 4·4 (± 0·3) min per host compared with 2·9 (± 0·3) min ($Z=3{\cdot}4$, $P<0{\cdot}0007$).

Impala significantly decreased their rate of self grooming during the time when oxpeckers were in attendance on them. Table 1 compares grooming by impala when oxpeckers were in attendance with grooming by impala in the absence of attending oxpeckers. In the dry season, grooming rates when oxpeckers were attending were 64–79% lower than when oxpeckers were absent; in the wet season, grooming rates with oxpeckers attending were 79–89% lower than in the absence of oxpeckers. These differences were highly significant in both seasons (Mann-Whitney test, Table 1).

Discussion

Yellow-billed oxpeckers at Matobo foraged 30–35% of the time that they attended impala, and this percentage remained consistent throughout the year.

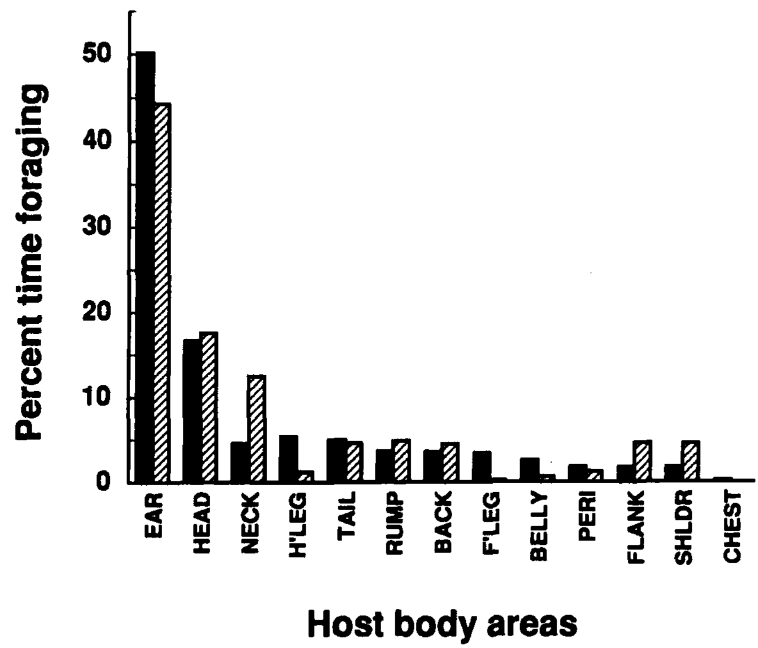

Fig. 2. The body areas of impala that were foraged upon by oxpeckers during the dry season (October–November 1992; solid bars) and the wet season (March–April 1993; cross-hatched bars) at Matobo National Park. Body areas are: ears, head, neck, hindleg, tail, rump, back, foreleg, belly, perineum, flank, shoulder, and chest.

Table 1. Grooming per h (mean ± SE) of impala when oxpeckers were in attendance compared to grooming rate of female impala when oxpeckers were not in attendance at Matobo National Park, and *Z*- and *P*-values for Mann–Whitney comparisons

Grooming per h	Oxpeckers present	Oxpeckers absent	*Z*	*P*
Dry season				
Self-oral bouts	2·68 (± 0·70)	7·48 (± 1·20)	3·4	0·0006
Self-oral episodes	36 (± 12)	99 (± 18)	3·2	0·001
Scratch bouts	0·39 (± 0·17)	2·03 (± 0·32)	4·1	0·0001
Scratch episodes	12 (± 5)	51 (± 9)	3·8	0·0002
Wet season				
Self-oral bouts	3·89 (± 0·91)	17·82 (± 1·88)	5·8	0·0001
Self-oral episodes	45 (± 12)	282 (± 48)	5·6	0·0001
Scratch bouts	0·62 (± 0·32)	3·39 (± 0·52)	4·1	0·0001
Scratch episodes	6 (± 3)	70 (± 13)	4·2	0·0001

For their part, impala hosts tolerated the foraging attentions of oxpeckers 86% of the time. Of tolerating impala, 42% exhibited active accommodation behaviour (lowering an ear, inclining the head, or standing still), while the remaining 58% were indifferent to the attentions of the birds. A high toleration of oxpeckers and pronounced accommodation movements by impala to facilitate foraging efforts was also reported for red-billed oxpeckers in East Africa (Hart *et al.*, 1990).

Oxpeckers were attracted to larger groups of impala insofar as there was a positive correlation between impala herd size and oxpecker flock size. This makes sense in terms of foraging economy because the larger the host group size, the more oxpeckers that can be supported. The fact that oxpecker flock size increase was not proportional to the increase in impala herd size (i.e. there were fewer oxpeckers per impala in larger groups) suggests that one benefit to oxpeckers of larger herds would be increased numbers of hosts per oxpecker by means of a dilution effect. Although the dilution effect of grouping generally benefits ungulate hosts by reducing the per capita risk of predation or parasitism from flying insects in larger groups (Mooring & Hart, 1992b), in this case impala in larger herds were at a disadvantage because each impala received less foraging attention from oxpeckers than they would have in a smaller herd.

The ears were the single most preferred foraging site for yellow-billed oxpeckers, representing up to 50% of foraging time on impala. Hart *et al.* (1990) reported similar results for red-billed oxpeckers foraging upon impala in Kenya, with 34% of foraging directed to the ears, more than any other body part. At Matobo, foraging sessions on the ears were also significantly longer than sessions directed to other body areas. This is of interest in view of the preponderance of adult ticks (67%) collected from the ears of patch-sampled female impala and the high percentage of impala with heavy infestations of immature ticks in the ears. Male and female impala harboured 75–77% of adult ticks on the ear, head, and neck region, which was where oxpeckers directed 71–74% of their foraging efforts. Impala are unable to reach the ear, head, and neck for self-oral grooming, which may explain the greater concentration of ticks found on this region. Although impala direct scratching and allogrooming to the ears, head, and neck, scratching is unlikely to be as effective in removing ticks as oral grooming with the teeth (Mooring, 1995), and, because the ears are pliant and yield to oral grooming, allogrooming is probably less efficient for tick removal from the ears than is foraging by oxpeckers. Interestingly, red-billed oxpeckers in Kenya directed 72% of foraging on impala to the ear, head, and neck (Hart *et al.*, 1990). This pattern would be adaptive for oxpeckers in terms of optimal foraging efficiency.

Vegetational tick sampling established that adult tick challenge at Matobo was considerably greater at the end of the wet season compared with the end of the dry season. Oxpeckers have been shown to be almost 100% effective in removing adult stage ticks (Bezuidenhout & Stutterheim, 1980), and adult ticks would be their preferred food items compared with the smaller larval and nymphal stages. Because engorging adult ticks (especially females) are able to remove far more blood from the host than immatures, adult ticks represent the greatest cost of tick infestation to hosts. Oral grooming with the teeth would be most efficient at removing the larger adults, and previous work has shown that adult ticks are the primary determinant of impala self-grooming rates (Mooring, 1995).

Female impala observed during the same time frame as part of another study (Mooring, 1995) exhibited significantly higher rates of self-oral and scratch grooming during the wet season compared with the dry season (Fig. 3).

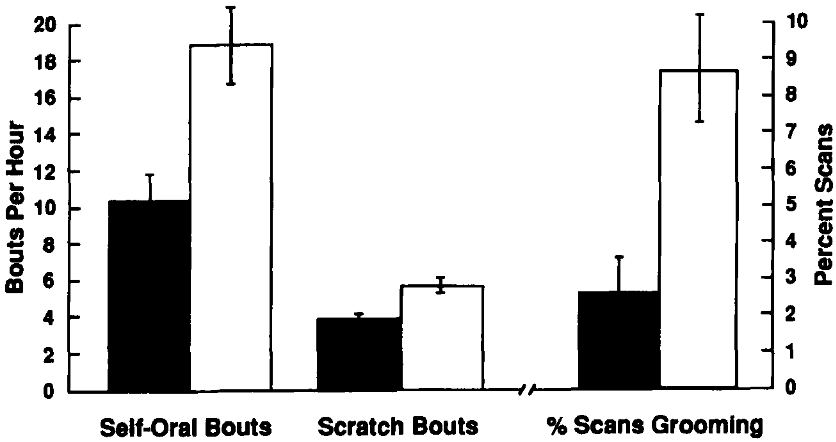

Fig. 3. Mean (±SE) self-grooming bouts per h and percent scans grooming by impala at Matobo National Park during the dry season (October–November 1992) (solid bars) and the wet season (March–April 1993) (open bars). Data from Mooring (1995).

Presumably, this increase in grooming rate was in response to increased tick burdens on the impala during the wet season. In support of this, rates of self-oral grooming and scratching by impala at Kyle Recreational Park in Zimbabwe were positively correlated with adult tick challenge throughout the year (Mooring, 1995). Due to the seasonal variation in tick burden on impala hosts, oxpeckers spent 72% more time foraging during the dry season compared with the wet season. It is suggested here that oxpeckers in the low-tick dry season were forced to spend more time searching for the fewer ticks on their hosts, whereas in the high-tick wet season they became satiated more quickly by the greater tick load on impala.

Oxpecker foraging appears to reduce the amount of tick-control grooming effort needed for impala to avoid excessive infestation. Grooming rate was reduced during the time that oxpeckers were present upon impala hosts. (Because impala in the presence of oxpeckers were observed only while the focal oxpecker attended the host, an average of about 3–4 min, it cannot be said if there was a residual effect whereby grooming rate remained depressed for a period of time after the oxpecker departed.) Grooming is costly to impala in terms of saliva loss, distraction from vigilance, and attrition of the dental elements (Mooring, 1995), and oxpeckers are effective in removing ticks from the ears, head, and neck, areas not efficiently groomed by impala because they are not accessible to self-oral grooming. Attempting to groom with an oxpecker on the head or neck might also entail an additional energetic cost to the impala and interfere with grooming behaviour. When oxpeckers are in attendance, it is probably more energetically cost-effective from a tick-removal standpoint for impala to reduce their grooming in favour of tolerating and accommodating the foraging activity of oxpeckers.

There is a complex network of relationships between oxpecker, host, and tick burden, with oxpeckers and hosts benefiting mutually from their association. Oxpecker foraging is influenced by impala tick load and host response (tolerance or rejection), and the grooming behaviour of impala is influenced by the effectiveness of oxpecker tick removal. From the point of view of wildlife management, the results presented here indicate that impala populations, at least, would benefit from the presence of oxpeckers, both in terms of more effective tick control on the ear, head, and neck area, and by reducing the costs of grooming behaviour. Future studies may reveal similar benefits for other host species.

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References

ALTMANN, J. (1974) Observational study of behavior: sampling methods. *Behaviour* **49,** 227–267.

ATTWELL, R.I.G. (1966) Oxpeckers, and their association with mammals in Zambia. *Puku* **4,** 17–48.

BEZUIDENHOUT, J.D. & STUTTERHEIM, C.J. (1980) A critical evaluation of the role played by the red-billed oxpecker *Buphagus erythrorhynchus* in the biological control of ticks. *Onderstepoort J. Vet. Res.* **47,** 51–75.

BREITWISCH, R. (1992) Tickling for ticks. *Natural History*, March 1992, 56–63.

COLE, M. (1992) Oxpecker gets old job back. *BBC Wildlife* **10,** 58.

DALE, J. (1992a) The effect of the removal of buffalo *Syncerus caffer* (Sparman 1779) on the host selection of yellow-billed oxpeckers *Buphagus africanus* Linnaeus 1766 in Zimbabwe. *Trop. Zool.* **5,** 19–23.

DALE, J. (1992b) *The Foraging Ecology of Red-billed Oxpeckers* Buphagus erythrorhynchus *and Yellow-billed Oxpeckers* B. africanus *in Zimbabwe*. Unpubl. report, Department of National Parks and Wild Life Management, Zimbabwe.

GROBLER, J.H. (1976) The introduction of oxpeckers into Rhodes Matopos National Park. *Honeyguide* **87,** 23–25.

GROBLER, J.H. (1979) The re-introduction of oxpeckers *Buphagus africanus* and *B. erythrorhynchus* to the Rhodes Matopos National Park, Rhodesia. *Biol. Conserv.* **15,** 151–158.

GROBLER, J.H. & CHARSLEY, G.W. (1978) Host preference of the yellow-billed oxpecker in the Rhodes Matopos National Park, Rhodesia. *S. Afr. J. Wildl. Res.* **8,** 169–170.

HART, B.L. (1990) Behavioural adaptations to pathogens and parasites: five strategies. *Neurosci. Biobehav. Rev.* **14,** 273–294.

HART, B.L., HART, L.A. & MOORING, M.S. (1990) Differential foraging of oxpeckers on impala in comparison with sympatric antelope species. *Afr. J. Ecol.* **28,** 240–249.

HART, B.L. & HART, L.A. (1992) Reciprocal allogrooming in impala, *Aepyceros melampus*. *Anim. Behav.* **44,** 1073–1083.

HART, B.L., HART, L.A., MOORING, M.S. & OLUBAYO, R. (1992) Biological basis of grooming behaviour in antelope: the body-size, vigilance and habitat principles. *Anim. Behav.* **44,** 615–631.

KAISER, M.N., SUTHERST, R.W. & BOURNE, A.S. (1991) Tick (Acarina: Ixodidae) infestations on zebu cattle in northern Uganda. *Bull. Entomol. Res.* **81,** 257–562.

LIGHTFOOT, C.J. & NORVAL, R.A.I. (1981) Tick problems in wildlife in Zimbabwe. 1. The effects of tick parasitism on wild ungulates. *S. Afr. J. Wildl. Res.* **11,** 41–45.

Mooring, M.S. (1995) The effect of tick challenge on grooming rate by impala. *Anim. Behav.* **50,** 377–392.

Mooring, M.S. & Hart, B.L. (1992a) Reciprocal allogrooming in dam-reared and hand-reared impala fawns. *Ethology* **90,** 37–51.

Mooring, M.S. & Hart, B.L. (1992b) Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* **123,** 173–193.

Mooring, M.S. & Hart, B.L. (1993) The effect of relatedness, dominance, age, and association on reciprocal allogrooming by captive impala. *Ethology* **94,** 207–220.

Mooring, M.S. & Hart, B.L. (1995) Differential grooming rate and tick load of territorial male and female impala, *Aepyceros melampus. Behav. Ecol.* **6,** 94–101.

Mooring, M.S., Mazhowu, W. & Scott, C.A. (1994) The effect of rainfall on tick challenge at Kyle Recreational Park, Zimbabwe. *Exp. & Appl. Acarol.* **18,** 507–520.

Mulilo, J.B. (1985) Species quantification and seasonal abundance of ticks (Acarina: Ixodidae) in the eastern province of Zambia: ticks from cattle. *Trop. Pest Manage.* **31,** 204–207.

Mundy, P. (1983) The oxpeckers of Africa. *Afr. Wildl.* **37,** 111–116.

Norval, R.A.I., Sutherst, R.W., Kurki, J., Gibson, J.D. & Kerr, J.D. (1988) The effect of the brown ear-tick *Rhipicephalus appendiculatus* on the growth of Sanga and European breed cattle. *Vet. Parasitol.* **30,** 149–164.

Norval, R.A.I. & Lightfoot, C J. (1982) Tick problems in wildlife in Zimbabwe. Factors influencing the occurrence and abundance of *Rhipicephalus appendiculatus. Zimbabwe Vet. J.* **13,** 11–20.

Stutterheim, C.J., Mundy, P.J. & Cook, A.W. (1976) Comparisons between the two species of oxpecker. *Bokmakierie* **28,** 12–14.

White, J. (1990) Of eagles and oxpeckers. *The Farmer*, October 4 1990, p. 12.

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