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Red-billed oxpeckers: vampires or tickbirds?

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Many recent studies have shown that classic examples of mutualism are either far more complicated than originally believed, or that they are not mutualisms at all. Red-billed oxpeckers (*Buphagus erythrorhynchus*) are just such an example of an ''adaptive story.'' These small birds feed almost exclusively on what they can glean from the skin of large African mammals. The relationship is obligate for the birds, and it is generally assumed that hosts benefit through a reduction in tick load. Although widely accepted in the literature, this theory has never been tested in the field. I excluded oxpeckers from cattle as part of a controlled field experiment in Zimbabwe to test this idea. Changes in adult tick loads were unaffected by excluding the birds. In addition, oxpeckers significantly prolonged the healing time of wounds and removed earwax. These results suggest that the oxpecker–mammal relationship is more complex than was previously thought. *Key words: Buphagus erythrorhynchus,* continuum, earwax, ixodid ticks, mutualism, oxpeckers. *[Behav Ecol 11:154–160 (2000)]*

Red-billed oxpeckers (*Buphagus erythrorhynchus*) feed almost exclusively on what they can collect from the skin of large African mammals. Their diet includes ixodid ticks, dead skin, mucus, saliva, blood, sweat, and tears (Bezuidenhout and Stutterheim, 1980). Ticks are costly parasites because they drain blood, inflict bites, and are vectors for many diseases (Howell et al., 1978). It is thought that tick removal must be beneficial to the host mammals, and the relationship between oxpecker and mammal is therefore believed to be a mutualism (Bezuidenhout and Stutterheim, 1980; Moreau, 1933; Mundy, 1992; Someren, 1951). Yet evidence for beneficial tick reduction is usually either anecdotal (Pitman, 1956), or inferred (Breitwisch, 1992; Someren, 1951). Mooring and Mundy (1996), for instance, showed that the congeneric yellow-billed oxpeckers (*Buphagus africanus*) feed on those areas of an impala where the animal cannot groom itself (head, neck, and ears), and that these areas have significantly heavier tick loads than the rest of the body. They went on to argue that this demonstrates the oxpecker's role in tick control. Yet their result indicates only that impalas are better at reducing their own tick loads than are oxpeckers, which they achieve by grooming themselves with their teeth, a behavior shown to be extremely effective at reducing tick loads (Mooring et al., 1996).

Stutterheim et al. (1988) provided some experimental evidence. They artificially infested two oxen with a known number of adult ticks of different species and put them in a pen with five red-billed oxpeckers. The birds significantly reduced the tick loads over a period of 7 days. While this demonstrated which tick species oxpeckers prefer to eat (blue ticks, *Boophilus decoloratus,* and brown ear ticks, *Rhipicephalus appendiculatus*), it did not show what effect oxpeckers might have in the field where ticks are attaching continuously to the host, oxpeckers will always have the option of other hosts to feed on, and where there is unlikely to be a ratio as high as five birds to two hosts 24 h a day.

Although tick feeding has been the focus of much attention, the oxpecker's habit of feeding at open wounds has generally been ignored (e.g., Stutterheim et al., 1988), or regarded as having a negligible effect (e.g., Dale, 1992), despite strong evidence that blood is the birds' preferred food (e.g., Bezuidenhout and Stutterheim, 1980; Weeks, 1999). Some authors have even argued that this behavior may be beneficial to mammals because it keeps the wound clean and prevents both bacterial infection and infestation by *Calliphoridae* blowflies (Breitwisch, 1992; Someren, 1951).

What is needed is an experiment similar to the ones carried out on cleaner fish (Grutter, 1996, 1999), where the cleaner is excluded from a group of hosts and the effects compared to a control group. If the birds do provide tick reduction benefits, then we should expect to see a significant increase in the numbers of ticks on the experimental animals. If blood is the favored food, however, then we might predict that the controls will have significantly more wounds than animals relieved of oxpecker attention.

In this paper I present results from a field experiment designed to test the effects of excluding oxpeckers on their hosts. The work was carried out in the lowveld of southern Zimbabwe on red-billed oxpeckers and a small herd of domestic cattle.

METHODS

I worked on Sentinel Ranch, a private property in the lowveld of Zimbabwe (29°E, 22°S). Annual rainfall averages 332 mm, and mean maximum temperatures range from 35°C in the summer to 24°C in winter. Sentinel Ranch has a large population of red-billed oxpeckers that feed both on game and a study herd of 22 Bonsmara oxen (the Bonsmara is a South African variety of cow, a cross between *Bos taurus* and *Bos indicus*). Up to 60 individual birds visited the *kraal* (cattle enclosure) every morning, where they would spend approximately 2 h feeding on the animals. Small groups of oxpeckers continued to visit and feed on the oxen in the field throughout the day (Weeks, 1998).

Cattle are hosts to five species of ixodid tick at Sentinel (blue ticks, brown ear ticks, bont ticks *Amblyommma hebraeum,* red-legged ticks *Rhipicephalus evertsi,* and bont-legged ticks *Hyalomma marginatum*). Ticks have three life stages (larva, nymph, and adult), each of which requires a different individual host on which they attach and engorge with blood before dropping off and metamorphosing to the next stage. The exception is the one-host blue tick, which goes through its entire life cycle (a process that takes roughly 4 weeks) on a single host. Adult male ticks of all species spend up to a month attached to their host; adult females are attached for about 1 week.

For the experiment, I arbitrarily divided the herd into 2 groups of 11 animals, experimentals and controls. For the first

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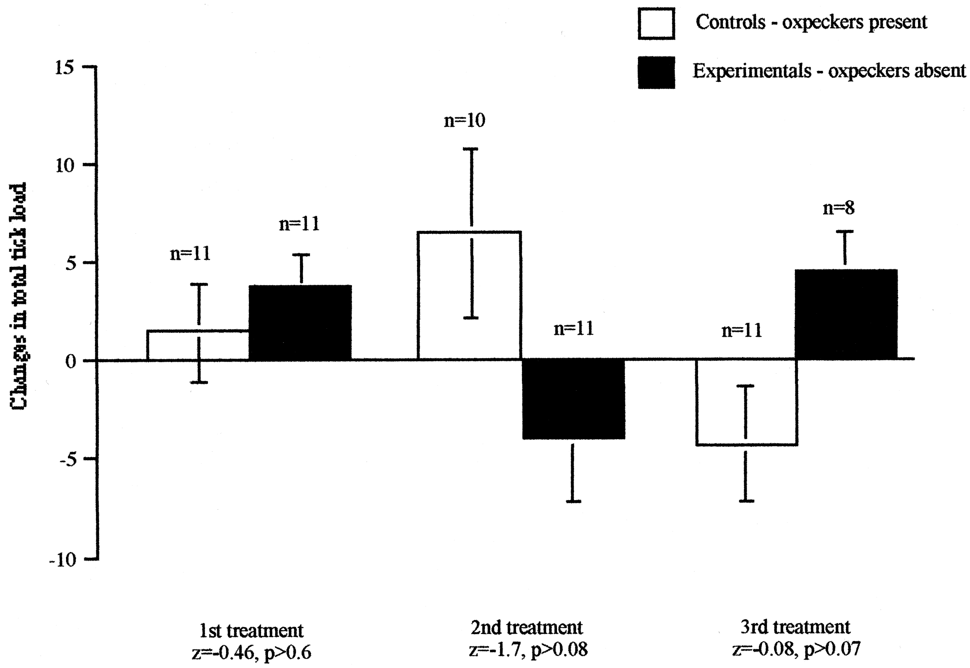

Figure 1
The magnitude and direction of change in mean total tick load (±SE) for Control and experimental oxen for each replicated experiment (Mann-Whitney test throughout).

treatment (21 November–18 December 1996), I excluded oxpeckers from the experimental group for 4 weeks. Because adult ticks are continuously attaching to the hosts and their drop-off rate is low, this period would have been sufficient to detect any effect oxpeckers might have had on tick loads.

An assistant stayed with the herd throughout the day (oxpeckers do not feed during the night) and chased off any oxpeckers that attempted to land on the oxen. I remained with the control group, which oxpeckers continued to visit and feed on as normal. The two groups fed in two separate grazing areas, which I alternated every 2 days. They spent the night in separate cattle kraals, which I alternated every week. Controlling for grazing areas was particularly important because the ranch has large populations of other potential tick hosts, notably impala (*Aepyceros melampus*), eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), and warthog (*Phacochoerus aethipicus*). The density of ticks may therefore have varied from area to area. It is also important to note that the developmental period needed for engorged nymphal ticks to change into adult ticks is close to 2 months for brown ear ticks (see, e.g., Randolph, 1994, 1997) and the congeneric red-legged tick (Yassir et al., 1992), and is considerably longer for the other species (Norval et al., 1992; Petney et al., 1987; Rechav, 1982). This does not take into account the additional time required for the adult's cuticle to harden, the tick to start searching for a new host, and the delay while it finds a host. There was thus no danger of the results being confounded by cross-contamination between control and experimental herds.

For the second treatment (17 January–14 February 1997), I switched the groups so that the experimentals became controls and vice versa. For the third treatment (19 August–16 September 1997), I arbitrarily selected a different combination of oxen to fill the control and experimental groups. Although there were originally 22 oxen, 3 animals died during the year, so the sample size varies slightly between experiments.

For each animal, I counted all the adult ticks, identifying them to species level, and, for the bont ticks (*Ambylomma hebraeum*), to sex. I counted and mapped the number of open wounds (which I defined as any break of the skin >0.5 cm across that had no scab tissue protecting it). I also assigned an earwax score based on a visual assessment of the inner portion of the right ear using the following scale: 0 = no wax at all, spotless, only clean flesh visible inside the ear; 1 = yellow waxy glaze over part or all of the inner pinna; 2 = solid globules of yellow or orange wax present; 3 = ear thick with dark orange wax, no clean flesh visible. I repeated full tick counts, wound scores, and earwax measures on all animals every week. I only scored adult ticks, as there is no valid technique for counting larval ticks on a live animal (Mooring and McKenzie, 1995), and it is difficult and time consuming to look for nymphal ticks. Adults are also accurate gauges of the overall tick load of an animal (Mooring and McKenzie, 1995).

From monthly mean tick scores collected over a 12-month period, I found that the majority of adult ticks on any one animal were male bont ticks (mean = 69%; Weeks, 1998), a figure that might swamp the effects of other species. With all the tick analyses, therefore, I analyzed not only the overall changes in totals, but also the changes in species' totals.

I compared the median monthly change in tick loads between experimental and control oxen for each treatment and corrected for this multiple comparison with a sequential Bonferroni correction (Sokal and Rohlf, 1995). Because the data are not normally distributed, all my tests are nonparametric (Siegel and Castellan, 1988). All statistical tests are two-tailed with the significance level set at 0.05.

RESULTS

Ticks

Absence of oxpeckers had no significant effect on the change in total tick load in any of the three replicate experiments (Figure 1). Absence of oxpeckers also had little effect on infestation changes at the level of species and sex. In each treatment, there were six species/sex analyses plus the total tick comparison, giving a total of 21 possible significant results. Blue ticks did not appear in any of the three replicates, and brown ear ticks, a seasonal species, only appeared in the second. Of these 16 remaining results, only 1 showed a significantly greater increase on experimental oxen (Figure 2). No other comparison was significant (sequential Bonferroni cor-

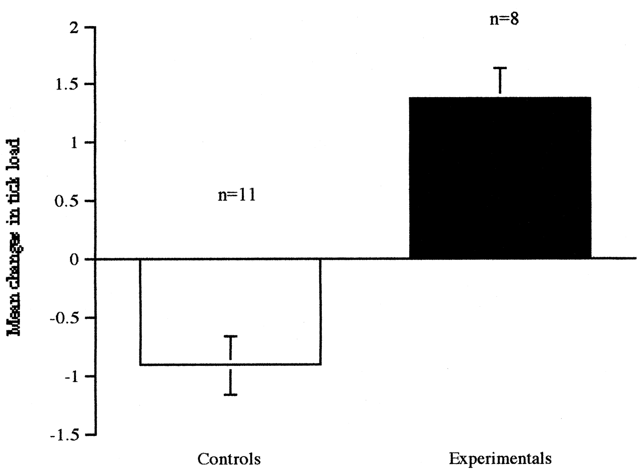

Figure 2
The magnitude and direction of change in mean tick load (±SE) for red-legged ticks between control and experimental oxen in the third experiment (Mann-Whitney test, $z = -3.09$, $p = .002$).

rection: Dunn-Sidak method, $k = 15$ comparisons, critical value = 0.0034). Total tick loads were low and never exceeded a mean of 30 ticks per animal in any of the treatments.

Wounds and earwax

I analyzed the wound scores in two ways. First, I compared the accumulation score of new wounds between the control and experimental groups (so an individual wound that appeared at any subsequent weekly check only counted as one wound for this analysis). Control cattle exposed to oxpeckers had significantly more wounds than experimental cattle in all treatments (Figure 3).

I also looked at what happened to individual wounds during the course of the experiment. Some completely healed and were not scored again. Others were still present the following week (persisted) or were seen again at least once in some other week (recurred). In two out of the three experiments, wounds on control oxen were significantly more likely to persist or recur during the course of the treatments than wounds on experimental cattle (Table 1). The nonsignificant result from the first treatment was probably due to the low number of initial wounds on the experimental herd.

In all three treatments, excluding oxpeckers resulted in a significant increase of ox earwax (Figure 4).

DISCUSSION

Contrary to expectations, excluding oxpeckers in this experiment did not cause an increase in tick loads on cattle. For each of the three replicate experiments, exclusion of oxpeckers could have resulted in changes in the total tick load, the load of five different species of tick, and the load of either sex of one of these species (bont ticks). In 20 out of these 21 comparisons, however (including total tick load), excluding oxpeckers had no effect. Even if the significant result is attributable to oxpeckers, the effect is not a consistent one.

These results are also consistent with focal watch results from the same study (Weeks, 1999) which show that oxpeckers spent more than 85% of their foraging time feeding on blood, in ears, or by scissoring their bills through the animal's hair. (It is not clear what oxpeckers are feeding on when they "scissor." It is generally assumed that they are searching for immature ticks, but my study suggests that they may be collecting flakes of dead skin. See Weeks, 1999, for more discussion of this question.) Observable tick feeding occupied less than 5% of total foraging time. Of course, this might simply be because ticks were scarce, forcing the oxpeckers to feed on wounds, but other studies, in areas with much higher tick densities, have also recorded wound feeding and found that observable tick feeding is low (e.g., Stutterheim et al., 1976). In any case,

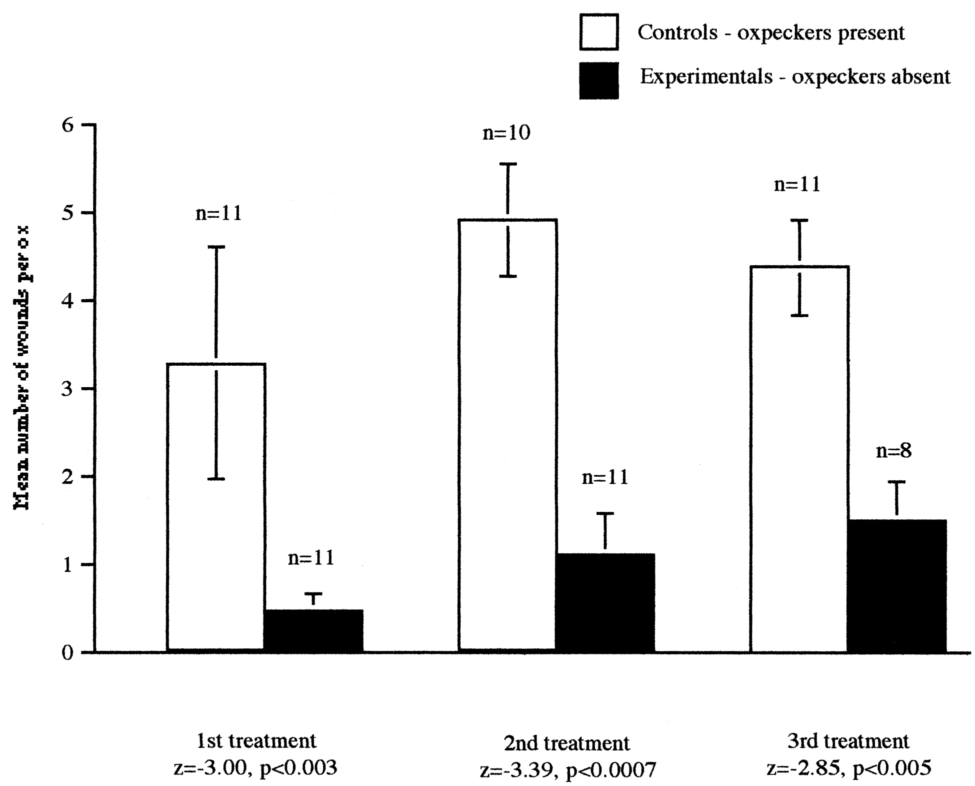

Figure 3
The mean number (±SE) of individual wounds per animal in all three treatments. In each case, control oxen had significantly more wounds than experimental ones (Mann-Whitney test throughout).

Table 1
Summary of the different wounds on control and experimental cows during the three treatments

	Persist/ recur	Heal	Totals	Fisher's Exact	
				ϕ	p
First treatment					
Controls	15	21	36		
Experimentals	1	4	5		
Totals	16	31	41	0.145	.6
Second treatment					
Controls	15	13	28		
Experimentals	0	12	12		
Totals	15	25	40	0.507	.001
Third treatment					
Controls	19	22	41		
Experimentals	0	10	10		
Totals	19	32	51	0.381	.008

there is strong evidence that blood is the birds' favored food, whether it is taken directly from a wound or in the form of an engorged tick (e.g., Bezuidenhout and Stutterheim, 1980; Weeks, 1999).

The results are also consistent with both my personal observations and those of others (e.g., Bezuidenhout and Stutterheim, 1980) that oxpeckers usually ignore ticks of all species which an observer, and presumably the birds, can clearly see. In fact, I would often see birds pecking at the place where the tick was attached to the host, making no attempt to remove it but instead trying to enlarge the break in the skin.

It could be argued that the Limpopo Valley is an unusually dry area with a low concentration of ticks and that oxpeckers are more likely to have an impact in areas of high tick infestations. This should certainly be tested, although Matson and Norval (1977) believe that oxpeckers would have a minimal effect in such places, arguing that the birds would simply not eat enough ticks to make a significant impact. Instead, they suggest that the birds are only likely to be effective at tick control in climatically marginal areas where ticks are tenuously established. They specifically suggest low rainfall areas in the lowveld (where this study was conducted) as fulfilling these criteria. Furthermore, Norval and Lightfoot (1982) have pointed out that the presence of oxpeckers has not prevented tick problems on game in seven high-rainfall game reserves in Zimbabwe.

In addition, oxpeckers are choosy about which ticks they eat, strongly preferring adult female blue ticks (Bezuidenhout and Stutterheim, 1980; Moreau, 1933; Stutterheim et al., 1988). This makes sense for the oxpecker because it is adult females that engorge with blood, but it is of no benefit to the host. By the time an oxpecker eats a fully engorged female blue tick, it has already bitten the host, passed on any diseases it is carrying, drained all the blood it is going to take, and, in

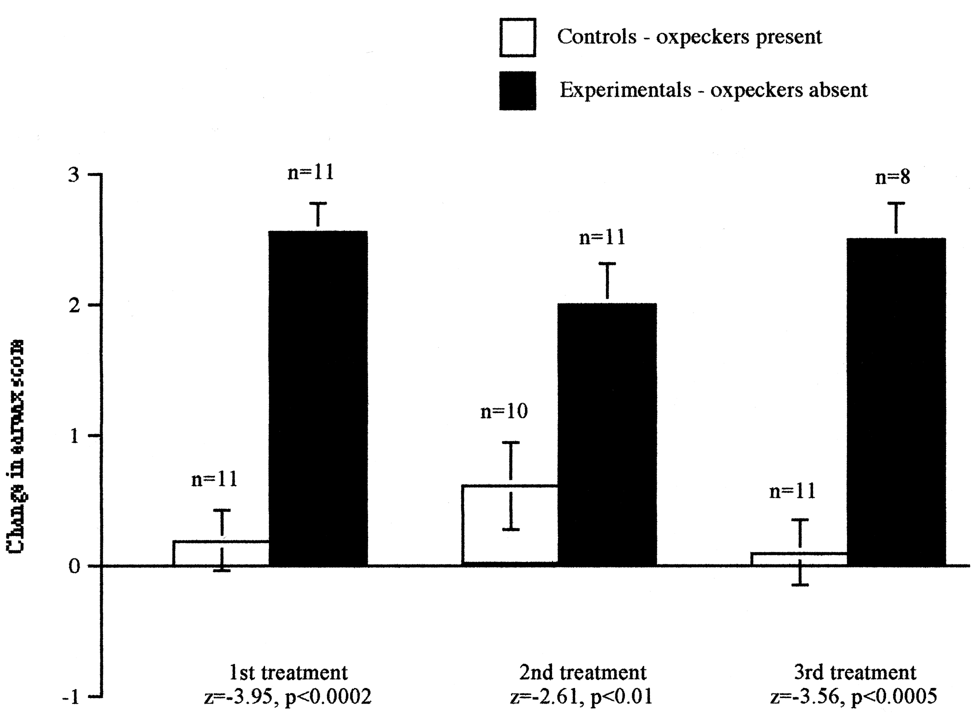

Figure 4
The mean changes (±SE) in earwax scores for control and experimental for each treatment (Mann-Whitney test throughout).

the case of blue ticks, has already gone through three life stages on the same individual host.

Nonetheless, we need to be cautious. Until recently, similar experiments on cleaner fish symbioses had failed to detect parasite reduction benefits to the host fish (Gorlick et al., 1987; Grutter, 1996, 1997; Losey, 1972; Youngbluth, 1968). The theory that cleaner fish really do clean (albeit one species of cleaner and one species of host) was only experimentally confirmed this year (Grutter, 1999). Much more work is needed on the oxpecker/mammal system before we can make definitive statements about mutualism and its extent. Perhaps oxpeckers chiefly benefit their hosts through removal of larval and/or nymphal ticks. Alternatively, the impact oxpeckers have on tick loads may vary with varying densities of the different tick species or between different tick species.

Wounds exploited by birds were usually the result of tick bites or scratches initially caused by barbed wire or acacia thorns (Weeks, 1998). These wounds rarely had time to form a healthy scab, often increased in size, and tended to persist for weeks at a time. Excluding oxpeckers resulted in significantly fewer wounds on experimental oxen in all treatments, and all but one of those wounds healed in less than a week. None of the wounds recurred in subsequent weeks.

Oxen with oxpeckers, by contrast, not only had a higher proportion of wounds that persisted or recurred, they also had a higher number of wounds overall. None of the wounds developed an infection or became infested by blowfly.

It is not known whether oxpeckers are able to create wounds on their hosts. Most of the wounds I recorded on the cattle were either the result of oxpeckers enlarging existing tick bites or clearly a scratch caused by a wire fence or an acacia bush that the birds were then able exploit. This does not exclude the possibility that oxpeckers can cause wounds, but I did not observe this in more than 2000 h of focal observations (Weeks, 1999), and it has not been recorded in the literature.

Deliberately inflicted or not, wound feeding is unlikely to be beneficial to the host mammal. It is hard, however, to quantify the possible fitness costs, or offset these costs against potential tick reduction benefits. The only evidence I have for this is the case of an oxen that had a tick bite on its sheath. The bite was first enlarged and then fed on regularly by oxpeckers for several weeks, eventually developing a swollen infection that prevented the ox from attaining an erection. It is hard to imagine a more direct blow to the fitness prospects of an animal.

Excluding oxpeckers caused a marked increase in earwax levels, suggesting that the birds are removing earwax, presumably to eat it. What benefits oxpeckers derive from eating earwax, and what effect, if any, this has on the oxen, are moot points. Earwax, or cerumen, consists of saturated, long-chain fatty acids (Sirigu et al., 1997) and is presumably high in energy. However, the structure of earwax also makes it difficult to digest (Place and Stiles, 1992). Other birds use wax as a source of a metabolic energy but may need a specialized digestive system to do so (Place and Stiles, 1992; Roby et al., 1986). It is not known whether oxpeckers possess this adaptation.

It is also not known whether earwax removal is beneficial or harmful for oxen. It is generally agreed that earwax provides physical protection for the external auditory meatus (e.g., Sirigu et al., 1997), while other authors (e.g., Sokolov et al., 1995) have shown that earwax in some carnivores has an antibacterial function. Furthermore, if earwax is high in energy, it may be costly to produce. Either way, its systematic removal by oxpeckers could be costly. Other work, mainly on humans, has shown that impacted earwax is a source of painful infection (e.g., Minja and Machemba, 1996), and heavy concentrations of earwax could also have a significant negative effect on an animal's hearing, a potentially serious effect for any animal that relies on sound to detect predators. Keeping the inner ear clean might therefore be beneficial.

CONCLUSION

Oxpeckers are unique among birds but not among the Chordata, being similar, in many ways, to the cleaner fish of coral reefs. Both systems involve a smaller, ''guest'' animal cleaning a larger host, or ''client,'' animal. Both oxpeckers and cleaner fish eat large numbers of parasites (ixodid ticks and gnathiid isopods, respectively), but they are also known to feed on their host's secretions (e.g., mucus) and to exploit lesions for flesh and blood (e.g., Bezuidenhout and Stutterheim, 1980; Gorlick et al., 1978). In addition, both interact with a wide variety of potential hosts.

In many ways, however, the cleaner fish system appears to be more elaborate. The strongest incidental evidence for mutualism with the fish is the existence of cleaning stations, small areas of the reef where the cleaner fish live, and which the host fish must choose to visit before the cleaners can feed. It is hard to see this as anything but evidence for mutualism (but see Losey, 1979). No such arrangement exists for oxpeckers, and the mammal hosts seem to have little control over the interaction (Weeks, 1999; but see Hart et al., 1990; Mooring and Mundy, 1996). Nor do host mammals solicit cleaning with specific displays or postures (though see Breitwisch, 1992) as many (but not all) host fish do (Gorlick et al., 1978).

The question of host preference has been studied in both systems, with no clear conclusions. Because host size is usually a reliable predictor of parasite load, we might expect a positive correlation between the size of the host and the preference of the cleaner. This is true for cleaner fish but appears to be a phylogenetic artifact (Grutter and Poulin, 1998). It is broadly true for oxpeckers (Koenig, 1997) but with some curious exceptions and with the added complication that oxpeckers also show a preference for hosts with manes (Koening, 1997). It is hard to draw general conclusions from either of these results.

Beyond this, the cleaner fish system is far better understood, if only because coral reef fish lend themselves to experimental manipulation rather more readily than large savannah herbivores. Until recently, exclusion experiments had failed to show parasite reduction benefits to host fish (e.g., Gorlick et al., 1987; Grutter, 1996; Losey, 1972), but Grutter (1999) has finally demonstrated that *Labroides* cleaners can significantly reduce parasite loads on one species of host fish. This last point is important because in the broader context of mutualism, most authors now agree that the costs and benefits of mutualisms lie on a continuum that may be influenced by various ecological factors (Bronstein, 1994; Pellmyr, 1989). A mutualism in one place or time may be a commensal or parasitic relationship in another area or at a different time of year. Mutualisms where more than two species are involved may be particularly prone to variation along this continuum (Bronstein, 1994; Gaume et al., 1998; Pellmyr, 1989). From this perspective, it is clear that we should expect great variation both in the cleaner fish symbiosis and in the oxpecker–mammal relationship, which not only involves many different species of tick, but a wide range of potential host mammals and two sympatric species of oxpecker.

So, although I was unable to detect tick reduction benefits at Sentinel Ranch, perhaps these occur in areas of greater tick density or where blue ticks, the preferred food tick, predominate. Alternatively, it is possible that oxpeckers are, for instance, parasitic on hippopotami (where they seem to feed exclusively on wounds: Attwell, 1966; Olivier and Laurie, 1974), commensal on impala, and mutualistic on rhinoceroses. Certainly, costs and benefits have been shown to vary within some mutualisms (e.g., Addicott, 1996; Pellmyr, 1989), and changes from parasitism/commensalism to mutualism and vice versa have been shown in both ant–aphid and mycorrhizal symbioses (Francis and Read, 1995; Gaume et al., 1998; Johnson et al., 1997; Sakata, 1995). Future work on oxpeckers should try to take these factors into account, although there remains the obvious logistic difficulty of obtaining the necessary data. It may also be necessary to look more closely at the hosts' ecology. Mammals that might otherwise be ideal hosts may be relatively underutilized by oxpeckers because they migrate or have huge home ranges or spend the day under water.

The available evidence, however, suggests that oxpeckers do not provide tick reduction benefits and that there may be costs associated with their habit of wound feeding. Further experimental evidence is required to see whether these results are the full story of oxpecker–mammal interactions or merely one end of a continuum of outcomes.

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