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Food choice, time budget and associated conflict between Yellow-billed Oxpeckers (*Buphagus africanus L.)* and Domestic Cattle Managers in Ibadan, Oyo state Nigeria.

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Abstract

The resultant conflict between the oxpeckers and cattle farmers/managers was explored. Food choice of yellow-billed oxpeckers (*Buphagus africanus*) in association with domestic cattle was assessed to determine the most utilized feed matter. The study was split into two: Firstly, oral interviews with 30 domestic cattle managers focused on human wildlife conflict between yellow-billed oxpeckers and domestic cattle managers. Six farms were identified through referrals and livestock managers were selected based on convenience. Secondly, we observed oxpecker behaviour within population of oxpeckers using University of Ibadan cattle farm as the observation station. Repeated observations were carried out to determine the preferred food choice of the yellow-billed oxpeckers as well as time budget during each recorded activity. A total of 180 observations were made with 1179 oxpecker-cattle interactions documented in the morning (08:00–10:00) and in the evening (16:00–18:00), within 30 days in dry season. Interactions were further grouped into feeding and non-feeding interactions. Feeding interactions was further split into wound and non-wound feeding. Interview responses showed a significant level of conflict with 86.36% of domestic cattle managers surveyed indicating that they had tried to eliminate oxpeckers before because of wound causing/feeding behaviour. Wound feeding was the least occurring feeding interaction which only occurred 6% of the time. Non-wound feeding interactions (ticks, skin flakes, mucous, earwax) had 94% ratio of occurrence showing that oxpeckers are simply opportunistic feeders that utilize wounds to increase their foraging efficiency. Oxpeckers selected ticks and skin flakes more frequently than mucous, blood and earwax, perching was the most obvious non-feeding activity, headshake was the most common avoidance technique to wade off oxpeckers who preferred the hump and rump among other locations on domestic cattle. Sensitization of managers on the benefits of oxpeckers is necessary to reduce negativistic attitude towards the species.
Key Words: Food Choice, Yellow-billed Oxpecker, Feeding, Domestic Cattle, Behaviour, Conflict, Wound Feeding.

Introduction

Food is essential for birds to survive and reproduce, the former is scarce and not uniformly distributed, therefore food choice, is a strong determinant of a bird population life history, occurrence, reproductive and survival success (Peron and Grosset, 2014). Cleaning interactions are positive inter-species relationships in which one species removes and feeds upon parasites infesting the other species. These interspecific associations improve the forage efficiency of the birds because they get more food while expending less energy than birds without cleaning associations (Sazima *et al.,* 2012). Oxpeckers are known to utilize a wide variety of food sources, some linked with carnivorous tendencies. Feed matter utilized by yellow-billed oxpeckers vary from; ticks, lice, mites and insects, earwax, scurf cells, hair, to nose, eye and mouth mucous secretions, which they get from large ungulate mammals. This feeding interaction between yellow-billed oxpeckers (*Buphagus africanus* Linnaeus) and large herbivores can be classified as an example. These widespread interspecies cleaning interactions occurs both on land and in water, typically with two participant species aptly named: the cleaner and the host (Sazima, 2011). Different factors influence oxpecker feeding relationship and preference for large mammal hosts, but, abundance of food remains the primary influence (Diplock *et al*., 2018).

Large ungulate mammals such as Buffalos (*Syncerus caffer* Sparrman) and domestic cattle (*Bos taurus* Linneaus) provide a relatively higher ectoparasite abundance. The larger the ungulate host, the larger the external surface area, space and resources available for exploitation by ectoparasites. Because of their larger mass and surface area, these large-bodied ungulate species could harbour greater numbers of ticks, as well as a higher proportion of adult ticks (which take a larger blood meal than the immature stages), compared with smaller ungulate species. Larger hosts also have larger home ranges, travel longer distances, and may visit more diverse habitats than smaller species, all of which increase the likelihood of acquiring a diverse parasite fauna (Krasnov *et al*., 2004; Esser *et al*., 2016), important to oxpeckers.

Host species such as domestic cattle act as a microhabitat for macro-parasites such as arthropods and helminthes. During these cleaning interactions, cleaner species forage on ectoparasites they remove from the hosts. Tick feeding is generally regarded as beneficial to the ungulate host, (Ndlovu and Combrink, 2015) reducing their ectoparasite load. Oxpeckers benefit as well, gleaning parasites from the host, improving their foraging efficiency, as they gather more food while expending less energy. In addition to obtaining nutritional benefits, they also gain increasing protection from predators, have stable mobile perches and are sources of nesting material (body hair) (Goodale *et al*., 2017). This led to the categorization of the oxpecker–ungulate interaction as mutualism rather than parasitism, the former being an interspecific interaction in which each species received a net benefit (Sazima and Sazima, 2010).

However, oxpeckers can manifest harmful tendencies and capitalize on other food types found on hosts (Sazima and Sazima, 2010). These additional foods may include dead or live tissue, blood, secretions, organic debris (Sazima and Sazima, 2010, Sazima *et al*., 2012). The interaction between the host and the oxpeckers could thus be regarded as commensalism if tick feeding does not occur, with the oxpeckers benefiting entirely, and with no harm coming to the host. Opposing views suggests that oxpeckers may even be acting as parasites, ignoring available ticks and instead consuming host tissues (McElligott *et al*., 2004; Nunn *et al,* 2011; Plantan *et al*., 2012) and blood gotten from open wounds. Aside from the wound feeding

behaviour, it was also noted that oxpeckers prefer adult female blue ticks (*Rhipicephalus decolaratus* Koch). The ticks are of no direct benefit to the host, however their removal is definitely beneficial to both host and oxpeckers, throwing more support for the mutualistic view. It is obvious that by the time an oxpecker eats an engorged female blue tick, it has already bitten the host, transferred any disease it was carrying via oropharyngeal path and fed on the blood volume it needed (Weeks, 2000).

Previous research indicated that wound feeding by oxpeckers on wild hosts is rare, constituting just 3.1% of feeding activities (Plantan, 2009) probably due to the abundance of different species of ungulate hosts providing large numbers of ectoparasites, thereby removing the need for oxpeckers to parasitize ungulates directly. It could also be due to the effectiveness of resistance behaviour displayed by the wild ungulate host in preventing parasitism. Resistance behaviour is defined as a range of behaviour that either prevents oxpeckers initiating foraging, stops them foraging or alters the position of foraging on the body (Bishop and Bishop, 2014). Such behaviour includes movements of the body, legs, or head, and sometimes retreating (Sazima 2011; Sazima *et al*. 2012). For most parts of the African continent, wild ungulates such as buffalos, giraffes, elands *etc*. have largely been replaced by domestic cattle and their extant but highly reduced populations are now restricted to protected areas. It is not needless to say oxpeckers occur only in areas where their host are present, presenting themselves as obligate ungulate interactors. Domestic ungulates are supposedly quieter and more docile than their wild counterparts providing a more stable perch (Londei, 2016), suitable for foraging activities.

With the increase in number of cattle farms in rural or wooded vegetation zones, it is plausible that oxpeckers will keep thriving and conflict will increase because losses via secondary infections on cattle are more focused upon by livestock farmers. Oxpeckers, are often locally referred to as "vampire birds" by cattle ranchers are seen as a serious problem to the overall health of cattle as well as the overall management of the cattle ranch. During the preliminary survey, ranchers indicated their interest in eliminating the oxpecker population around their ranch. They had tried various methods over the years such as mechanical control (use of sticks, stones, rat gums attached to cattle back etc.) and chemical control (use of poisons, spraying of lethal compounds). The ranchers also noted that the risk of injuring the cattle stock remained the major reason they were cautious in applying long acting lethal chemicals. Oxpeckers have undergone serious range restrictions in most part of the African continent due to the increasing use of acaricides (mainly arsenical compounds) in cattle dips from 1902 onward. However, with the advent of new dipping compounds, lethal to ticks, but not the birds (Kalle *et al*., 2017), the previous global population decline of oxpeckers has been reduced. However, further decline in the extant patchy and fragmented populations must be monitored and prevented.

Plate 1: An adult Oxpecker wound feeding on the hump of a cow at University of Ibadan Cattle farm during our study Source: Field Work, 2018

The objective of this study is to understand the presence of conflict between farm managers and oxpeckers at livestock farms which would be detrimental to the small oxpecker population in southwest Nigeria. We also set out to understand the feeding interaction of oxpeckers with cattle and the most utilized feed matter as the second phase of the project.
We predict that human-oxpecker conflict is occurring and a basis for oxpeckers decline
We predict that tick feeding interaction of oxpeckers is a more significant part of their feeding compared to blood feeding

Materials and Methods

Study Area
A two-stage sampling protocol was used to select respondents in Ibadan, Oyo state. Farms were identified using Snow-ball technique, while convenience sampling was used to select respondents (domestic cattle managers) on the six farms identified. Only six farms were identified through referrals as there were no database of such farms at Oyo State and livestock managers were selected based on convenience. A Semi-structured questionnaire was administered by direct interview 30 times based on convenience to managers and farm assistants at six farms in Oyo state. The questionnaire was drafted to understand the presence of conflict between livestock managers and the oxpeckers.

The following determinant questions were asked in the questionnaire administered at the University of Ibadan Cattle farm, Akinyele market (Cattle rearing section), Institute of Agricultural Research and Training Cattle Farm, Lifeyield Farms, Kara Fiditi (Cattle rearing section) and Fasola Farms visited (Figure 1):
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(1) Do you perceive that the current oxpecker population is decreasing, stable or increasing
(2) Which of these relationships do you think oxpeckers have with your cattle (Parasitism) (Symbiosis) (Mutualism)
(3) In your opinion, are oxpeckers good or bad for your ranch (Good) (Bad)
(4) What do you perceive oxpeckers do to your cattle
(5) How do you control oxpeckers in your ranch

University of Ibadan Cattle Farm was selected as the focal point of interest for the behavioural study because it was the only suitable site with yellow-billed oxpeckers daily

interacting with cattle. Other cattle ranches explored in Oyo State either completely lacked oxpecker populations like the prominent Fasola Farms or the interaction between oxpeckers and cattle were too infrequent. Sites like Akinyele Cattle rearing Section and Bodija cattle rearing farms could not be utilized because human activity was always preventing the birds from approaching and oxpecker-cattle interactions were only seldom reported to occur within the farms. The study area where oxpecker cattle interactions were observed was the University of Ibadan Cattle Farm, which lies on latitude N $07^0$27'25.6" and longitude E $003^0$53'58.3, within the University environs, Oyo State, Nigeria. The farm is set up under the Faculty of Agriculture Teaching Farm to teach students practical applications of class lessons. The area is bound to the east by a Teak (*Tectona grandis* L.f.) plantation as well as an ever flowing stream and an abandoned water reservoir project. To the west of the farm is a tertiary forest separated by a tarred road. The farm has paddocks fenced and used in a rotatory manner. The paddock vegetation is abundant with grasses and shrubs. The climate of the area is tropical with two distinct seasons. The dry season (November to February) and the rainy season (March to October). The period of harmattan marks the driest part of the seasons. The average annual rainfall is 1311mm and maximum rainfall is in the month of September. Daily operations on the farm included cleaning of the enclosures before the cattle are allowed to move into paddocks to graze till noon when they are moved back into their enclosures. Water is provided in water troughs. Each enclosure floor is demarcated by cemented area and open sandy soil. Oxpeckers were seen sand-bathing in the sandy soils. The roofing of the enclosures only extends to cover the cemented portion of the floors while the sandy soil portion was exposed.

Data collection

Responses from livestock managers and assistants were collected based on convenience sampling from Six farms; University of Ibadan Cattle farm, Akinyele market (Cattle rearing section), Institute of Agricultural Research and Training Cattle Farm, Lifeyield Farms, Kara Fiditi (Cattle rearing section) and Fasola Farm) selected by snow-ball technique, a technique based on referrals where one practicing manager or farmer refers us to other practicing farms. Thirty (30) copies of a semi-structured questionnaire was administered to cattle farm managers and assistants by direct interview, ensuring information collected were independent. Data collected were based on socio-demographic characteristics, frequency of contact with oxpeckers, control mechanisms, perception and attitude towards oxpeckers. Data generated was used to determine farms where yellow-billed oxpeckers were present and level of conflict between the cattle ranchers and the oxpeckers.

The farm interview data highlighted several farms where cows were farmed in Ibadan, all farm were visited and University of Ibadan farm had the best opportunity to observe interactions of yellow-billed oxpeckers and cattle. Data was collected on oxpecker food choice by direct observation of the behavioural activities of yellow-billed oxpeckers on domestic cattle (*Bos taurus indicus*) to determine the time budget allocated to each feeding activity as well as other activities. Oxpeckers are continuous foragers with peak feeding periods. Observations were made during these peak feeding periods in the morning (08:00–10:00) and in the afternoon (16:00–18:00) (Ndlovu and Combrink, 2015). Feed matter utilized by oxpeckers as seen and recorded during the observations include: wound tissue, ticks, earwax, mucous and skin flakes. Observations were made using a Celestron 8x42 Nature DX binocular, and repeated every two minutes to measure time budgets expended on feeding and in particular food choice selected.

A yellow-billed oxpecker interacting with a cow was studied for two minutes from a distance using a pair of binoculars and this was recorded as one interaction (Table 1). Five separate interactions were documented during each observation which lasted 10 minutes. 3 observations were made per hour. A total of 180 observations were made over a period of 30 days from the month of October to November, 2018 which falls during the dry season. Categorizations of data fell under the feeding interaction, non feeding interaction, resistance behaviour from the cow, body location where interaction too place as shown in Table 1.

Data analyses

To determine associated conflict between oxpeckers and managers of domestic cattle, data from questionnaire was used to decide whether the conflict between oxpeckers and cattle farm was of high priority or not. Oxpecker interactions with domestic cattle were weighted as either good or bad or mutualistic versus parasitic. Frequency distribution was used to explore data retrieved from respondents (Figure 1, 2 and 3).

To determine food choice of yellow-billed oxpeckers, based on Table 1, a frequency distribution was carried out. Means along with standard errors and standard deviations are presented in Table 2. A graphical illustration was also made to show what food choice was more frequent was observed. A non-parametric one way analysis of variance (Kruskal-Wallis Test) was carried out on observed interactions of oxpeckers and domestic cattle, post hoc test were performed when distributions among the independent factors were significantly different (Table 2 and Appendix 1).

Table 1: Categorization of Oxpecker Cattle Interactions recorded.

Feeding Interactions	Non-Feeding Interactions	Resistance Behaviour	Body Location
Wound feeding	Preening	Skin shake	Rump
Tick feeding	Perching	Tail swish	Head
Mucous feeding	Calling	Head shake	Hump
Earwax feeding	Roosting	Leg stomp	Belly
Skin flakes feeding	Sand-bathing	Walk away	Sides

To determine time budget of yellow-billed oxpeckers, this was presented in a frequency distribution based on location of the body oxpeckers spent more of their time on the host animal, non-feeding activity and resistance behaviour of the cattle to oxpeckers when they were feeding or trying to feed. A non-parametric one-way analysis of variance (Kruskal-Wallis Test) was carried out on observed activity of oxpeckers and domestic cattle, post hoc test were performed when distributions among the independent factors were significantly different (Table 2 and Appendix 2, 3 and 4).

Table 2: Frequency distribution of Yellow-billed Oxpecker food choice, time budget, oxpecker avoidance, Oxpecker location and age observed at university of Ibadan cattle farm.

Food Choice		Wound	Tick	Earwax	Mucous	Skin Flakes	Kruskal-Wallis Test
N	Valid	180	180	180	180	180	$X^2_{(4)}$=265.371
	Missing	0	0	0	0	0	P<0.001
Mean		.22	1.27	.33	.23	1.65	
Std. Error of Mean		.044	.090	.046	.039	.102	

Std. Deviation	.584	1.208	.624	.530	1.368	
Time Budget	Perching	Preening	Roosting	Calling	Bathing	
Mean	1.48	.36	.06	.91	.04	$X^2_{(4)}$=322.741
Std. Error of Mean	.092	.048	.020	.083	.015	P<0.001
Std. Deviation	1.235	.648	.262	1.117	.207	
Avoidance	Skin Shake	Tail Swish	Head Shake	Leg Stomp	Walkaway	
Mean	.30	.21	.76	.06	.16	$X^2_{(4)}$=125.990
Std. Error of Mean	.044	.036	.069	.020	.031	P<0.001
Std. Deviation	.588	.484	.924	.262	.420	
Oxpecker Location	Rump	Head	Hump	Belly	Sides	
Mean	1.35	.78	1.36	.15	.82	$X^2_{(4)}$=197.819
Std. Error of Mean	.081	.082	.080	.032	.067	P<0.001
Std. Deviation	1.091	1.101	1.076	.429	.894	

Oxpecker Age	Adult	Juvenile
Mean	1.24	.03
Std. Error of Mean	.157	.012
Std. Deviation	2.110	.165

Results

Presence of significant level of Human-Wildlife Conflict

Of the 23 cattle rearers who had previous knowledge about oxpeckers, majority (91.30%) indicated that they perceived that the relationship between oxpeckers and cattle was parasitism which is detrimental to cattle (Figure 2) or that oxpeckers were bad for their ranch (95.65%). Most of the cattle rearers (60%) alluded to the fact that oxpeckers caused Injury to cattle while feeding (Figure 3). Cattle rearers seemed to be unsure of the current status of oxpeckers though 66.7% perceived the population was declining. Also, of the majority of respondents that worked or had worked in a farm where oxpeckers were present, 86.36% indicated that they had tried at one time or the other, to control oxpeckers on their farms through mechanical means (use of stones, sticks etc.) and chemical means (application of chemicals) as opposed to a minority (13.64%) that said they had never tried to control the oxpeckers on their farms

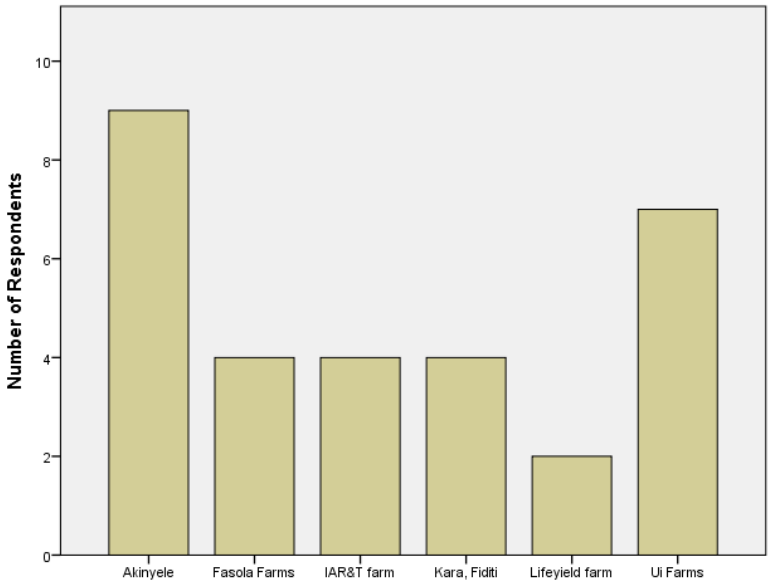

Figure 1: Cattle Farm Locations where Questionnaire was administered

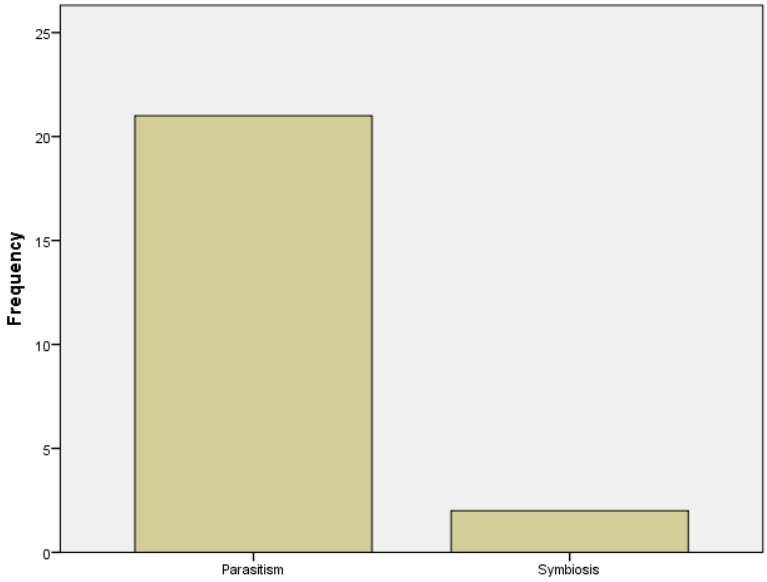

Figure 2: Respondents Categorization of Oxpecker-Cattle Relationship

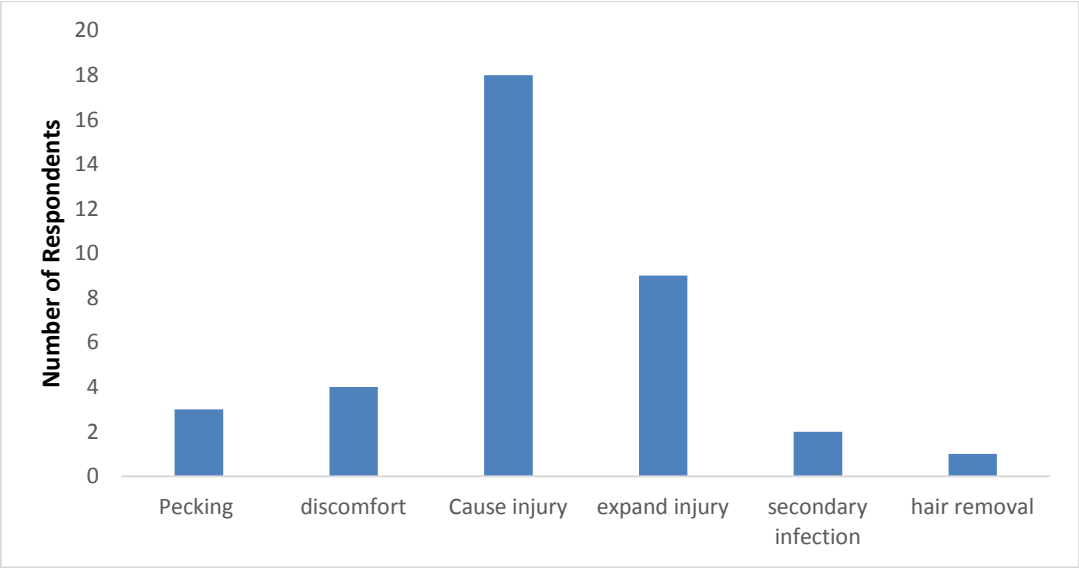

Figure 3: Perceived impact of oxpeckers on domestic cattle by cattle managers in Oyo State, Nigeria

Yellow-billed oxpeckers-Cattle interactions

Upon analysis of recorded observations for feeding behaviour, skin flakes were the most preferred feed matter with a mean frequency of 1.65 occurrence per hour (which is about 45% occurrence). Ticks followed with a mean of 1.27 (which is about 34.32% occurrence). Earwax feeding had a mean frequency of 0.33 (about 8.92% occurrence), Mucous feeding had a mean of 0.23 (6.22%) while wound feeding had a mean of 0.22 (5.95%) (Figure 4). Non-feeding behaviour were also analysed to determine the mean frequency of occurrence for each observation and Perching was the most prevalent behaviour having a mean frequency of occurrence of 1.48 followed by calling activities which had a mean occurrence of 0.91. Next prevalent activity was preening with a mean of 0.36 while Roosting and Sand bathing were the least prevalent activity with mean frequencies of 0.06 and 0.04 respectively (Figure 5). The resistance behaviour of domestic cattle to oxpecker interactions was analyzed. Shaking of the head was the most engaged resistance behaviour with a mean occurrence frequency of 0.76. Shuddering/shaking of the skin was the second most prevalent resistance behaviour with a mean occurrence of 0.30. Swishing of the tail was the next prevalent

resistance activity with a mean occurrence of 0.21 while walking away and stomping of the leg were the least with mean occurrences of 0.16 and 0.06 respectively (Figure 6). Body location preferences of oxpeckers on Cattle after analysis showed that the hump was the most preferred body location with a Mean frequency of 1.36. The rump had a mean frequency of 1.35 followed by the Sides of the cattle which had a mean frequency of 0.82 and the head with a mean frequency of 0.78. The least preferred body location was the belly having a mean frequency of 0.15 (Figure 7).

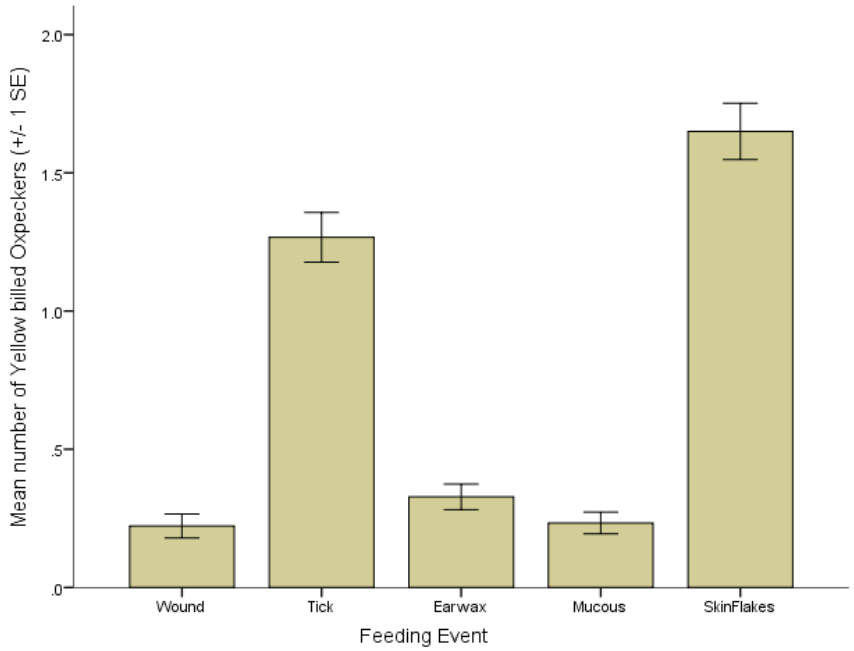

Figure 4: Comparison of mean frequencies of oxpecker feeding behaviours

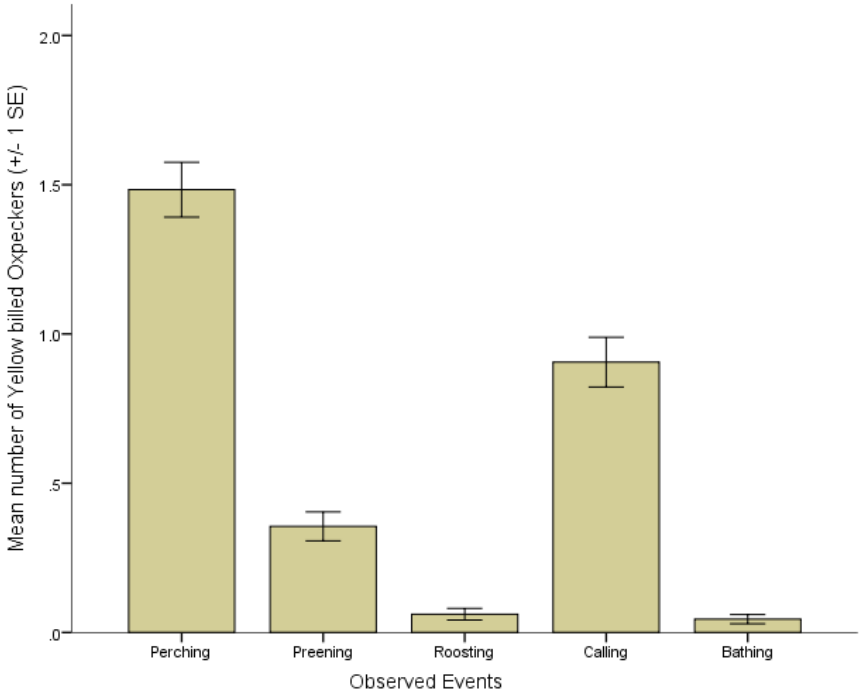

Figure 5: Comparison of mean frequencies of oxpecker non-feeding behaviour

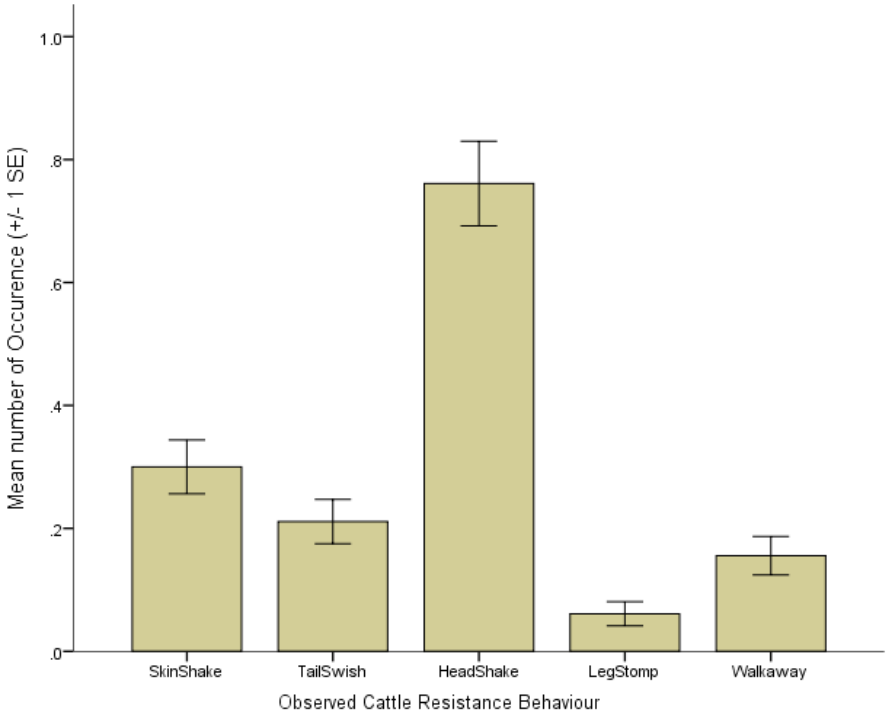

Figure 6: Comparison of mean occurrences of cattle resistance behaviours to oxpecker interactions

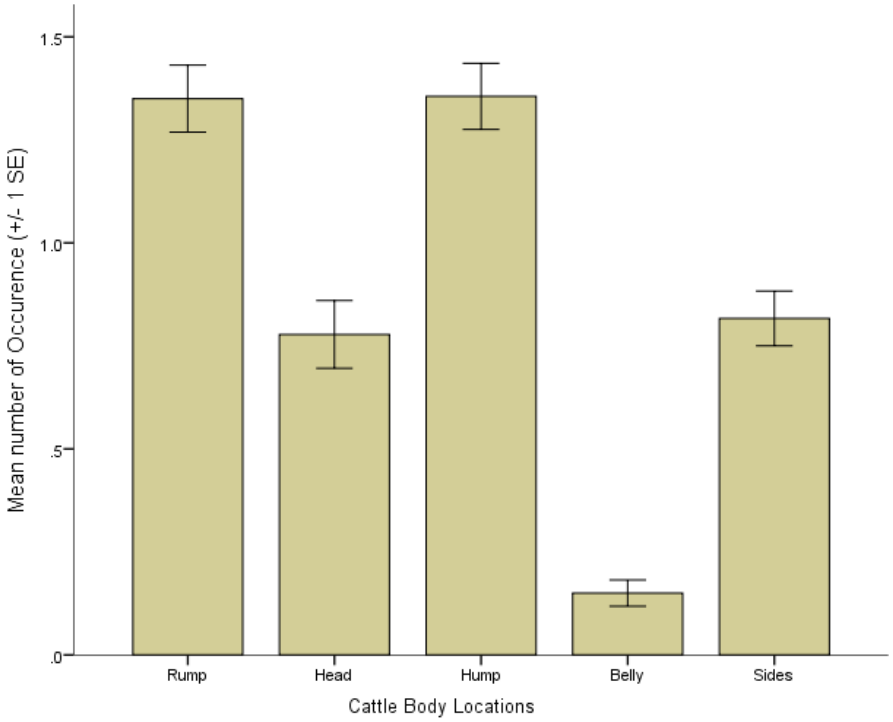

Figure 7: Comparison of the mean occurrences of body locations of oxpecker cattle interactions

Discussion

Human–wildlife conflict is an important conservation challenge because threats to human safety, livestock and property frequently trigger retaliatory killing of wildlife (Inskip and Zimmerman, 2009). Presence of conflict was proven by the questionnaire administered in the four farms (University of Ibadan cattle farm, Akinyele Market (Cattle rearing section), Kara Fiditi (Cattle rearing section) and Lifeyield farms) where the oxpeckers were reported present. University of Ibadan cattle farm workers noted in the questionnaire administered that the oxpeckers were perceived to cause and expand injuries on domestic cattle and make the animals uncomfortable. One of the respondents from Akinyele cattle rearing section noted that they were perceived to cause hair loss while another respondent indicated that oxpeckers are perceived to be responsible for secondary infections that occur after causing and expanding injuries. Overall, oxpeckers were persecuted because they were seen to cause injuries, expand injuries, delay healing of wounds, predispose cattle to secondary infections and cause discomfort for cattle. Responses also showed that farmers persecuted oxpeckers by using lethal chemical compounds, stoning the birds, using sticks and an interesting technique of rat gums attached to the cattle rumps to trap the birds.

Time budget for feeding proves that oxpeckers spend a significantly higher time foraging on skin flakes and ticks. Wound feeding interactions only occurred 40 times (6%) during the 180 observations with 666 recorded feeding interactions between cattle and oxpeckers. Our results support that oxpeckers only feed on wounds very rarely when the opportunity occurs, and the mutualism/parasitism dynamism of the oxpecker-cattle relationship may be driven by the availability of ticks and other potential food sources. This result is in tandem with the research results of Plantan in Shingdwedzi, South Africa, where wound feeding occurred 3.1% of 558 observations (Plantan, 2009). The research of Ndlovu and Combrink (2015) also recorded exceedingly low occurrences of wound feeding by red-billed oxpeckers and the absence of wound feeding in yellow-billed oxpeckers suggesting that wound feeding behaviour is also not prevalent in South Africa as previously reported in cattle ranches in Zimbabwe (Weeks, 2000). Skin flakes were the most utilized feed matter during the study with feeding interactions that occurred 297 times (45%) and tick feeding interactions that occurred 228 (34.23%) times. Earwax feeding interactions occurred 59 times (8.9%) while mucous feeding occurred 42 times (6.31%).

It also supports that the frequency of feeding interactions that cause wounds, expand injuries, delay healing and predispose cattle to secondary infections is much lower than cattle farmers assume and the local nickname ‘Vampire bird’ may be unjustified. The cattle population showed a good level of resistance behaviour that should dissuade any bird from prolonged and harmful feeding. Oxpeckers are very essential in the management of ticks. Tick infestation of a domestic cattle host can ensure 25kg of the carcass weight is lost at slaughter due to blood loss and appetite loss, because the tick’s saliva contains a toxin that suppresses appetite (Farmers Weekly Website, 2019). Ticks also carry diseases that affect cattle’s reproductive organs and damage their skin, reducing the grade of their leather quality (Farmers Weekly Website, 2019). Ticks pose a significant economic burden to Livestock Agriculture. Farmers in South Africa are reporting that they prefer oxpeckers to forage on the ectoparasite load of their cattle as ticks are constantly building resistance to their cattle dips alternatives.

Conclusion

The presence of conflict between cattle farmers and yellow-billed 0xpeckers in South west Nigeria as shown by our study alludes to the misconception 'oxpeckers are blood suckers'. We posit that the perceived threat of the oxpeckers to domestic cattle as observed from our data is significantly minimal. Wound feeding is an opportunistic behaviour that is manifested when a host is injured. However, this only occurs rarely and should not be a cause of human conflict with the birds. Observations from our study show that the resistance behaviour shown by Cattle to oxpecker interactions discourages wound feeding. oxpeckers also spend more time utilizing skin flakes and ticks as feed matter compared to blood. However, birds are innately wired to increase foraging efficiency whist limiting search time. It is easy to see why oxpeckers could capitalize on a wound where they can easily obtain highly nutritious food matter such as blood and tissue while completely minimizing search time. Removal of ticks from the environment through chemical control measures would inhibit oxpecker populations in any region, and could shift the oxpecker–ungulate relationship away from mutualism and towards parasitism.

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Appendix 1: **Pairwise Comparisons of Feeding groups**

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.
Wound-Mucous	-8.492	24.109	-.352	.725	1.000
Wound-Earwax	-35.731	24.109	-1.482	.138	1.000
Wound-Tick	-240.256	24.109	-9.966	.000	**.000**
Wound-Skin Flakes	-289.869	24.109	-12.023	.000	**.000**
Mucous-Earwax	27.239	24.109	1.130	.259	1.000
Mucous-Tick	231.764	24.109	9.613	.000	**.000**
Mucous-Skin Flakes	-281.378	24.109	-11.671	.000	**.000**
Earwax-Tick	204.525	24.109	8.483	.000	**.000**
Earwax-Skin Flakes	-254.139	24.109	-10.541	.000	**.000**
Tick-Skin Flakes	-49.614	24.109	-2.058	.040	.396

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same. Asymptotic significances (2-sided tests) are displayed. The significance level is .05. Significantly different comparisons in bold.

Appendix 2: Pairwise Comparisons of Non-feeding groups

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.
Bathing-Roosting	4.883	22.766	.215	.830	1.000
Bathing-Preening	95.636	22.766	4.201	.000	**.000**
Bathing-Calling	217.586	22.766	9.558	.000	**.000**
Bathing-Perching	335.506	22.766	14.737	.000	**.000**
Roosting-Preening	90.753	22.766	3.986	.000	**.001**
Roosting-Calling	-212.703	22.766	-9.343	.000	**.000**
Roosting-Perching	330.622	22.766	14.523	.000	**.000**
Preening-Calling	-121.950	22.766	-5.357	.000	**.000**
Preening-Perching	239.869	22.766	10.536	.000	**.000**
Calling-Perching	117.919	22.766	5.180	.000	**.000**

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same. Asymptotic significances (2-sided tests) are displayed. The significance level is .05. Significantly different comparisons in bold.

Appendix 3: Pairwise Comparisons of Resistance groups

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.
Leg Stomp-Walkaway	-34.225	19.754	-1.733	.083	.832
Leg Stomp-Tail Swish	53.931	19.754	2.730	.006	.063
Leg Stomp-Skin Shake	80.381	19.754	4.069	.000	**.000**
Leg Stomp-Head Shake	204.700	19.754	10.362	.000	**.000**
Walkaway-Tail Swish	19.706	19.754	.998	.318	1.000
Walkaway-Skin Shake	46.156	19.754	2.337	.019	.195
Walkaway-Head Shake	170.475	19.754	8.630	.000	**.000**
Tail Swish-Skin Shake	26.450	19.754	1.339	.181	1.000
Tail Swish-Head Shake	-150.769	19.754	-7.632	.000	**.000**
Skin Shake-Head Shake	-124.319	19.754	-6.293	.000	**.000**

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same. Asymptotic significances (2-sided tests) are displayed. The significance level is .05. Significantly different comparisons in bold.

Appendix 4: Pairwise Comparisons of Body location groups

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.
Belly-Head	152.519	25.532	5.974	.000	**.000**
Belly-Sides	-185.681	25.532	-7.272	.000	**.000**
Belly-Rump	305.047	25.532	11.948	.000	**.000**
Belly-Hump	307.128	25.532	12.029	.000	**.000**
Head-Sides	-33.161	25.532	-1.299	.194	1.000
Head-Rump	152.528	25.532	5.974	.000	**.000**
Head-Hump	-154.608	25.532	-6.055	.000	**.000**
Sides-Rump	119.367	25.532	4.675	.000	**.000**
Sides-Hump	121.447	25.532	4.757	.000	**.000**
Rump-Hump	-2.081	25.532	-.081	.935	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same. Asymptotic significances (2-sided tests) are displayed. The significance level is .05. Significantly different comparisons in bold.