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Factors influencing host selection by yellow-billed oxpeckers at Matobo National Park, Zimbabwe

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Summary

Oxpecker host selection appears to be governed by an array of factors affecting the efficiency of foraging for ticks, with optimally foraging oxpeckers choosing those hosts that maximize tick intake and/or minimize search time. We studied yellow-billed oxpeckers *Buphagus africanus* (Linnaeus) at Matobo National Park, Zimbabwe, in order to examine the relationship between host selection and seasonal tick abundance, host characteristics and water availability. Preference ranks were highly correlated between the dry and wet seasons, implying that relative tick burdens of host species did not change appreciably. The selection index (a measure of oxpeckers per host) and the density index (a measure of oxpecker density on host body surface) showed a threefold increase from dry season to wet season for all host species, presumably due to greater tick burdens on hosts during the wet season. Host selection indices were positively correlated with species-typical host body mass, indicating that oxpeckers selected larger-sized hosts that supported higher densities of ticks. A negative correlation between host preference and herd size during the wet season suggested that oxpeckers optimize foraging efficiency by choosing larger herds when attending smaller-bodied hosts. Hosts observed at a water source appeared to be more attractive to oxpeckers than those surveyed where water was not available.

Key words: foraging, hosts, oxpecker, selection, ticks, Zimbabwe

Résumé

La sélection des hôtes par le pique-boeuf semble obéir à toute une gamme de facteurs touchant l'efficacité de la recherche de tiques, les meilleurs pique-boeufs choisissant des hôtes qui maximisent la prise de tiques et/ou diminuent le temps de recherche. Nous avons étudié les pique-boeufs africains, *Buphagus africanus* (Linnaeus), au Parc National de Matobo, au Zimbabwe, pour examiner la relation entre le choix de l'hôte et l'abondance saisonnière de tiques, les caractéristiques de l'hôte et la disponibilité en eau. Les ordres de préférence étaient très liés entre la saison sèche et la saison des pluies, impliquant que la quantité relative des tiques des espèces hôtes ne changaient pas de façon

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appréciable. L'index de sélection (dénombrement des pique-boeufs par hôte) et l'index de densité (mesure de la densité de pique-boeufs sur la surface de l'hôte) montraient un triplement pour toutes les espèces hôtes entre la saison sèche et la saison des pluies, sans doute dû au plus grand nombre de tiques sur les hôtes pendant la saison des pluies. Les index de sélection des hôtes étaient positivement liés à la masse corporelle de l'espèce, indiquant que les pique-boeufs choisissaient les hôtes plus gros, qui portaient les plus grandes densités de tiques. Une corrélation négative entre la préférence des hôtes et la taille des troupeaux pendant la saison des pluies suggérait que les pique-boeufs optimisaient l'efficacité de leurs prélèvements en choisissant les plus gros troupeaux lorsqu'ils s'occupaient de plus petits animaux. Les hôtes observés près d'un point d'eau semblaient plus attractifs pour les pique-boeufs que ceux qui étaient observés là où il n'y avait pas d'eau.

Introduction

Oxpeckers (Buphaginae) are African tick birds well known for their symbiotic relationship with wild ungulates (Mundy, 1983). By removing ticks from mammalian hosts oxpeckers gain the major food item in their diet (Attwell, 1966; Bezuidenhout & Stutterheim, 1980) and hosts benefit from reduced tick burdens (Mooring & Mundy, 1996). Both the red-billed oxpecker *Buphagus erythrorhynchus* (Stanley) and the yellow-billed oxpecker *B. africanus* (Linnaeus) select a limited number of ungulate species from the total range of species available in the environment (reviewed by Hart, Hart & Mooring, 1990). When present, certain host species are always highly preferred by oxpeckers, while other species are rarely, or never, selected. These observations led to the notion that oxpeckers are predisposed to select certain host species, and that 'key hosts' are needed to maintain an oxpecker population (Grobler, 1980). A number of studies over the years have attempted to quantify host preferences by counting numbers of hosts and attending oxpeckers in order to compute a preference index. The results of these studies have confused the concept of inherent preferences by revealing wide discrepancies in preference for the same host species in different locales and preference changes following the removal of key hosts (Hustler, 1987; Dale, 1992a).

Rather than host preferences being somehow pre-programmed, it may be that selection of hosts by oxpeckers is governed by a number of factors that influence oxpecker foraging for ticks (Grobler, 1980; Hart *et al.*, 1990), with oxpeckers under selection pressure to optimize foraging efficiency by choosing those hosts that maximize tick intake and/or minimize search time. Factors likely to play a role in host selection by optimally foraging oxpeckers may be divided into those relating to intrinsic characteristics of the host animal, those relating to characteristics of ticks found on hosts and those relating to environmental factors impacting the likelihood of encountering tick-bearing hosts.

Of the numerous host factors that may interact to make a host more or less attractive to oxpeckers, body mass is perhaps the most significant (Hart *et al.*, 1990). Because of their greater mass relative to surface area, members of large-bodied species tolerate greater absolute 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 species (Horak, 1982; Horak *et al.*, 1983). Larger-bodied species also appear to support a higher density of ticks per unit surface area (Hart *et al*., 1990; Olubayo *et al*., 1993). Besides preference for members of larger species, oxpeckers may choose larger individuals within a species (Dale, 1992b). If body mass is an important factor determining host selection by oxpeckers, analysis of data from past studies should show a robust correlation between oxpecker host preference and body mass of hosts, as was previously shown for red-billed oxpeckers by Hart *et al*. (1990).

Typical herd size of hosts would be expected to influence host selection because the larger the size of the herd the less time would be required for oxpeckers to find another host individual once tick numbers on the current host animal were too few for foraging to be cost effective. Because smaller-bodied hosts carry fewer ticks, tick numbers would be depleted below the cost effective threshold sooner on smaller hosts and there should thus be a tendency for the mean herd size of selected hosts to be inversely related to body mass (smaller hosts should be found in larger herds).

Hair length is an intrinsic host factor that can influence oxpecker foraging efficiency by affecting search time for ticks (Grobler & Charsley, 1978; Grobler, 1980). In general, the shorter the hair, the easier it is for oxpeckers to locate and retrieve ticks from the pelage of hosts, while long hair increases search time and impedes tick removal.

Other host factors include the typical behavioural response of hosts to foraging by oxpeckers, which probably plays an important role in which species oxpeckers learn to select (Grobler, 1980; Hart *et al*., 1990). A host animal can respond to oxpecker foraging attempts by either rejecting the oxpecker or tolerating its presence; toleration may either be indifferent or involve active accommodation (Mooring & Mundy, 1996). Host intolerance is one reason why oxpeckers are rarely seen attending waterbuck *Kobus ellipsiprymnus* Ogilby or elephant *Loxodonta africana* Blumenbach (Stutterheim, 1980; Watkins & Cassidy, 1987; Dale & Hustler, 1991; Dale, 1992b; Mooring, 1993). The habitat preferences of hosts influence the rate at which ticks are acquired by animals, with woodland habitat generally supporting more ticks than grassland (Grobler, 1980; Hart *et al*., 1990). Finally, the relative availability of alternative host species in an area will have an impact on host selection (Dale 1992a, b).

Aside from intrinsic host characters, tick abundance and species of ticks carried by hosts should be a prime factor influencing oxpecker foraging and host selection. In Africa, environmental tick abundance varies dramatically between seasons and from year to year as a result of rainfall variation and other factors (reviewed by Mooring, Mazhowu & Scott, 1994), in turn affecting the tick burdens on host animals (Mulilo, 1985; Kaiser, Sutherst & Bourne, 1991; Olubayo *et al*., 1993). Because previous studies of oxpecker host selection were usually conducted within a single season, the influence of tick availability variation on host preferences has never been adequately addressed. Hosts should support more oxpeckers per animal during the tick-dense wet season (when ungulates carry higher tick loads) compared with the dry season. In addition to numbers of ticks, oxpeckers may have preferences for certain species of ticks and therefore choose hosts that support preferred tick species (Stutterheim & Brooke, 1981; Stutterheim, 1982).

If oxpeckers utilize certain environments, or if hosts are more likely to be discovered in certain habitats, suitable hosts that frequent such areas would be preferentially selected by oxpeckers. Environmental factors include proximity of hosts to water and visibility of hosts in a given habitat. Host species are attracted to water sources to drink, where host congregations may be denser, more reliable and more visible to oxpeckers than in other areas (Dale, 1992b). Hosts are more likely to be selected when in habitat types that increase the visibility of hosts to oxpeckers, such as in open grassland versus closed woodland (Dale, 1992b).

In order to approach oxpecker host selection as an integration of factors that optimize the efficiency of foraging for ticks, we must address the issue of how to best represent 'host preference'. The traditional measure of preference is based upon the number of oxpeckers per host animal, but host species vary in size and surface area available for ticks and thus are not directly comparable. To control for host size we considered it necessary to introduce an alternative measure of host preference based upon the number of oxpeckers per unit body surface area (i.e. oxpecker density).

Understanding the dynamics of host selection by oxpeckers is important not only for better understanding of oxpecker biology, but also for applied conservation of wildlife populations. Serious tick problems exist in many national parks and game farms in Africa (Norval & Lightfoot, 1982), and the introduction of oxpeckers to control tick burdens naturally on wild hosts is increasingly being attempted (Grobler, 1976, 1979; Mundy, 1983; White, 1990; Cole, 1992). Basic knowledge of the factors influencing oxpecker host selection is fundamental to the success of such introduction exercises. The purpose of this study was (a) to monitor host selection by oxpeckers at the same site during the wet and dry seasons (when tick availability varied) in order to examine the effect of environmental tick pressure on host selection, (b) to investigate the relationship between host preference and body mass, group size, hair length and water availability, (c) to re-analyse data from previous studies in order to further examine the influence of host body mass on host selection, and (d) to compare measures of host preference based upon oxpecker density on hosts versus oxpeckers per host.

Materials and methods

Study site

The study was conducted within the Whovi Wilderness Area (game park) of Matobo National Park, Zimbabwe (20°30′S, 28°30′E), which has been the site of several previous studies of oxpecker host selection (Grobler, 1976, 1979; Grobler & Charsley, 1978; Dale, 1992a, b). The game park has an area of 106 km^2. Field work was carried out from 20 October to 26 November 1992 (late dry season, when tick numbers are low) and from 3 March to 10 April 1993 (late wet season, when tick numbers are high). Yellow-billed oxpeckers at Matobo were estimated to number around 200 birds (Dale, 1992a). A small population of red-billed oxpeckers also exists at Matobo, representing 1–4% of the total oxpecker population (unpublished data). Observations focused on the yellow-billed oxpecker.

Counts of hosts and oxpeckers

Road counts were made from a vehicle and on foot from the road system in the game park. Ungulate hosts that supported oxpeckers at Matobo (and population estimates from the Department of National Parks, as reported by Dale (1992a)) were: white rhino (*Ceratotherium simum* (Buchell) (33), zebra *Equus burchelli* (Gray) (120), giraffe *Giraffa camelopardalis* Linnaeus (40), wildebeest *Connochaetes taurinus* (Burchell) (170), impala *Aepyceros melampus* (Lichtenstein) (800), warthog *Phacochoerus aethiopicus* (Pallas) (250), eland *Taurotragus oryx* (Pallas) (26), kudu *Tragelaphus strepsiceros* (Pallas) (60) and sable *Hippotragus niger* Harris (60). Black rhino *Diceros bicornis* (Linnaeus) were sighted during the wet season only.

When ungulate hosts were encountered the number and species of host animals and the number and ages of any attendant oxpeckers were recorded. Oxpecker age (adult or immature) was determined by bill colour according to Stutterheim, Mundy & Cook (1976). The censusing protocol established in previous studies (e.g. Dale, 1992a) was employed: oxpeckers that arrived on a host after initial sighting was made were ignored, if oxpeckers flew from one species to another after the initial sighting the oxpeckers were recorded only with the initial species, and repeat sightings of hosts were recorded only after at least 3 h had elapsed.

In order to investigate the possible influence of water availability on host selection, counts of oxpeckers and impala hosts were recorded at Mpopoma Dam during behavioural observations conducted in conjunction with two other studies (Mooring, 1995; Mooring & Mundy, 1996). Impala were the only host species consistently sighted at the dam. A total of 203 observation sessions totalling 61 h was completed. The number of oxpeckers and impala from all observations were summed for each season for calculation of the selection index (see below).

Selection index

Host selection by oxpeckers has traditionally been computed using the 'preference index' described by Grobler & Charsley (1978), which is calculated by dividing the number of host individuals sighted by the number of oxpeckers seen on them. The resulting index represents the number of host animals supporting one oxpecker. Interpretation of the preference index is confusing however, because smaller values indicate larger numbers of oxpeckers per host, i.e. higher preference. For convenience, we computed the number of oxpeckers per host (i.e. the inverse preference index) and multiplied by 100, a measure we shall term the 'selection index'. Counts of both species of oxpeckers were combined for calculation of selection indices. Because 99% of all oxpeckers sighted in the two seasons were the yellow-billed oxpecker (27 red-billed, 2008 yellow-billed), selection index values effectively represent host selection by yellow-billed oxpeckers.

Density index

In order to calculate a measure of oxpeckers per unit body surface area of hosts, we divided the selection index by species-typical body mass raised to the

Table 1. Number of individuals seen (number of sightings) of oxpeckers and hosts at Matobo National Park during the dry season 1992 and wet season 1993, and the selection index for each host species

Host species	Dry season			Wet season		
	Oxpeckers	Hosts	Selection index[1]	Oxpeckers	Hosts	Selection index[1]
White rhino	126 (56)	204 (91)	61·8	114 (19)	49 (23)	232·7
Black rhino	—	—	—	9 (1)	5 (3)	180·0
Giraffe	156 (54)	340 (104)	45·9	250 (39)	242 (70)	103·3
Eland	11 (5)	34 (7)	32·4	74 (11)	72 (11)	102·8
Zebra	97 (51)	620 (98)	15·6	374 (87)	1486 (157)	25·2
Sable	47 (15)	409 (37)	11·5	24 (7)	100 (13)	24·0
Kudu	5 (2)	76 (13)	6·6	6 (1)	33 (10)	18·2
Warthog	12 (7)	314 (100)	3·8	29 (9)	573 (137)	5·1
Wildebeest	27 (13)	1037 (109)	2·6	264 (57)	2412 (144)	10·9
Impala	17 (15)	2178 (212)	0·8	48 (19)	1939 (106)	2·5

[1]Selection index = (oxpeckers/hosts) × 100.

allometric exponent of 0·67 in order to convert mass to relative surface area, as described in Hart *et al.* (1990). For convenience, this value was then multiplied by 100 and termed the 'density index' because it is a representation of oxpecker density on host body surface.

Statistical analysis

For correlation of the selection and density indices with host species parameters, species-typical mass (mean of males and females) and hair length were taken from Skinner & Smithers (1990); 'biomass' was computed as the mean host herd size multiplied by species-typical mass. Correlation analysis was by Spearman rank-order correlation. When a specific prediction had been made as to the direction of the correlation (positive or negative), the test was one-tailed. All statistical analysis made use of non-parametric procedures (Siegel & Castellan, 1988) performed on BMDP Version 7.0 (BMDP Statistical Software, 1992). Data on yellow-billed oxpecker host selection were taken from five previous studies, conducted at Matobo (Rhodes Matopos) National Park, Zimbabwe (Grobler & Charsley, 1978; Dale, 1992a, b) and Hwange National Park, Zimbabwe (Hustler, 1987; Dale, 1992b). Data from Sinamatella and Robins were combined for Hustler (1987). Numbers of oxpeckers and terrestrial hosts utilized by oxpeckers were converted into selection indices for each species and correlated against species-typical mass using Spearman rank-order correlation.

Results

Ten host species were utilized by oxpeckers during the dry and wet seasons (Table 1). Selection indices in the dry season and wet season were highly correlated with one another (Spearman, $r_s = 0{\cdot}98$, $P < 0{\cdot}001$), and the selection ranks of the 10 species were, with one exception, identical in both seasons. In order of decreasing preference, oxpeckers attended rhinos most of all, followed by giraffe, eland, zebra, sable, kudu, warthog and wildebeest, with impala the

Table 2. Body mass and hair length of host species, and density index and mean herd size of hosts in the dry season 1992 and wet season 1993 at Matobo National Park

Host species	Body mass (kg)[1]	Hair length (mm)[1]	Dry season		Wet season	
			Density index[2]	Herd size	Density index[2]	Herd size
White rhino	1875	Naked	39·6	2·2	149·2	2·1
Black rhino	868	Naked	—	—	180·0	1·7
Giraffe	1010	9·5	44·6	3·3	100·3	3·5
Eland	555	13·9	83·1	4·9	263·8	6·6
Zebra	308	9·4	33·6	6·3	54·2	9·5
Sable	230	39·9	30·1	11·1	62·8	7·7
Kudu	190	20·1	19·6	5·9	54·1	3·3
Warthog	68	Sparse	22·5	3·1	30·2	4·2
Wildebeest	215	6·0	7·1	9·5	29·8	16·8
Impala	56	5·0	5·4	10·3	16·9	18·3

[1]From Skinner & Smithers, 1990.
[2]Density index = (selection index/body surface area) × 100.

least preferred. The one reversal involved warthog and wildebeest. Five black rhino were sighted in the wet season with a total of nine oxpeckers. Although none were sighted in the dry season, we assume that black rhinos would also have been used by oxpeckers in the dry season.

Host preferences based upon the alternative density index measure are listed in Table 2. As with the selection index, density indices were highly correlated with one another in the dry and wet seasons ($r_s = 0{\cdot}95$, $P < 0{\cdot}001$). According to the density index, eland were the most preferred host, supporting twice the density of oxpeckers on their body surface compared with white rhino (whereas according to the selection index white rhino supported twice as many oxpeckers per host as eland). Aside from eland being most preferred, density indices showed similar host preference ranks as the selection index. Three pairs of adjacently ranked host species exchanged density ranks between the seasons (white rhino/giraffe, zebra/sable, kudu/warthog).

Selection index values for all species were larger in the wet season compared with the dry season (Table 1; Wilcoxon, $P < 0{\cdot}004$), indicating that all host species had more oxpeckers in attendance per host animal. The mean (± standard error of the mean (SEM)) selection index was 20·1 (± 7·2) for nine species in the dry season and 70·5 (± 25·8) for 10 species in the wet season, representing more than a threefold increase in oxpeckers per host (as calculated from total number of oxpeckers and hosts sighted in each season). The appearance of immature (fledgling) oxpeckers in the wet season may have increased the number of oxpeckers in the study site, as 32% of the population at this time were immature ($N = 185$ immatures, 393 adults).

As with the selection index, density indices were higher in the wet season than the dry season for all host species (Table 2; Wilcoxon, $P < 0{\cdot}004$). The mean (± SEM) density index was 31·7 (± 7·4) in the dry season and 95·5 (± 24·5) in the wet season, indicating a threefold increase in oxpeckers per unit body surface area of hosts in the wet season compared with the dry season.

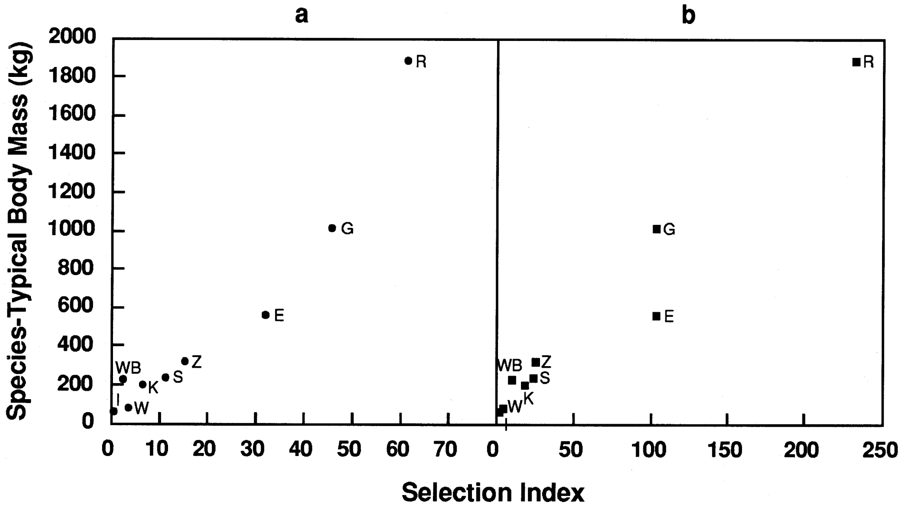

Fig. 1. Selection index values (a measure of oxpeckers per host) plotted against species-typical mass for nine host species utilized by oxpeckers at Matobo during (a) the dry season and (b) the wet season: R, white rhino; G, giraffe; E, eland; Z, zebra; S, sable; K, kudu; W, warthog; WB, wildebeest; I, impala. The selection index was positively correlated with body mass in both seasons (see text).

Selection indices (Table 1) were positively correlated with species-typical body mass (Table 2) for both the dry season (Spearman, $r_s = 0{\cdot}95$, $P < 0{\cdot}001$; Fig. 1a) and the wet season ($r_s = 0{\cdot}98$, $P < 0{\cdot}001$; Fig. 1b), meaning that the number of oxpeckers per host increased with greater host mass. There was also a positive correlation between the density index (Table 2) and body mass for the dry season ($r_s = 0{\cdot}87$, $P < 0{\cdot}005$; Fig. 2a) and the wet season ($r_s = 0{\cdot}88$, $P < 0{\cdot}005$; Fig. 2b), indicating that larger hosts were attended by a higher density of oxpeckers on the body surface.

During the wet season, host herd size (Table 2) was negatively correlated with both the selection index ($r_s = -0{\cdot}70$, $P < 0{\cdot}02$) and the density index ($r_s = -0{\cdot}64$, $P < 0{\cdot}05$). Host herd size during the dry season failed to show a significant negative correlation with either the selection index ($r_s = -0{\cdot}58$, $P < 0{\cdot}06$) or the density index ($r_s = -0{\cdot}53$, $P < 0{\cdot}08$).

Table 2 reveals that, except for sable, selected hosts had short to medium-length hair. There was no significant correlation between hair length and either measure of host preference (selection or density index) during either season. During the dry season, sparsely haired warthogs were more preferred as hosts (Table 1) than their small mass would otherwise indicate, being preferred above wildebeest of three times the weight. Except for kudu in the wet season, impala in the dry season and warthog in both seasons, biomass of the average herd of hosts exceeded 1000 kg, the mean (± SEM) host biomass being 2183 (± 301) kg.

The selection index for impala recorded at Mpopoma Dam was 3·1 (217 oxpeckers, 7110 impala) for the dry season and 4·8 (128 oxpeckers, 2671 impala) for the wet season. The selection index for impala at Mpopoma was 2–4 times larger than for impala in other areas of Matobo where water was not freely available (0·8–2·5, Table 1).

The results of the retrospective correlation analysis between yellow-billed oxpecker host preference and host mass were in agreement with this study, with

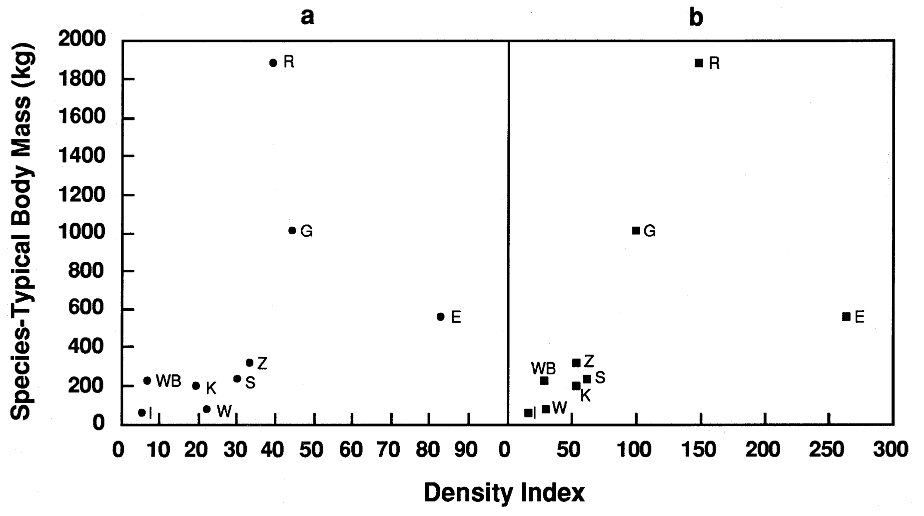

Fig. 2. Density index values (a measure of oxpeckers per unit body surface area) plotted against species-typical mass for nine host species utilized by oxpeckers at Matobo during (a) the dry season and (b) the wet season: R, white rhino; G, giraffe; E, eland; Z, zebra; S, sable; K, kudu; W, warthog; WB, wildebeest; I, impala. The density index was positively correlated with body mass in both seasons (see text).

all five studies yielding a significant positive correlation. The results were as folows: Grobler & Charsley (1978), N=9, r_s=0·82, P<0·02; Hustler (1987), N=9, r_s=0·73, P<0·05; Dale (1992a), N=8, r_s=0·95, P<0·002; Dale (1992b), Hwange, N=11, r_s=0·81, P<0·005; Dale (1992b), Matobo, N=10, r_s=0·92, P<0·001.

Discussion

At Matobo National Park, measures of host preference based upon yellow-billed oxpeckers per host and oxpeckers per unit body surface area identified similar host species preferences, with the exception of the most preferred host species. The selection index indicated that white rhino were preferred on a per host basis more than any other host species, and twice as much as eland. On the other hand, the density index identified eland as being the most preferred species in terms of density, with eland supporting twice the number of oxpeckers per unit surface area as white rhino. Thus, the density index provided information on host preference not evident from the selection index alone.

Because previous studies on oxpecker host selection were usually carried out within a single season, the role played by seasonal tick abundance could not be evaluated. Results from this study reveal that preference rankings of oxpeckers per host (selection index) were highly correlated, and virtually identical, between the dry and wet seasons. Measures of oxpecker density on hosts (density index) in the two seasons were also highly correlated, and all changes in rank involved exchanges with the adjacently ranked species. This implies that the relative tick burdens of hosts did not change appreciably between seasons. In the only other study to examine host selection across seasons, Grobler & Charsley (1978) found no seasonal variation in host selection over a 12-month period.

Although preference ranks were little changed between seasons, the number of oxpeckers per host animal and oxpeckers per unit body surface area increased for all host species from the dry season to the wet season, with hosts supporting a threefold increase in oxpecker numbers and density. From this we conclude that all host species supported more ticks during the wet season, thus attracting more oxpeckers per host. Data collected at Matobo during the same time period as this study (Mooring, 1995) showed that adult ticks were much more abundant in the environment during the wet season compared with the dry season, and we presume that hosts acquired greater tick burdens during the wet season. Although the appearance of fledgling oxpeckers during the wet season might also have contributed to greater numbers of oxpeckers per host, die-off of adult birds between seasons (currently unknown) could, by counteracting births, result in a steady-state population.

Host selection in terms of oxpeckers per host was highly correlated with species-typical body mass at Matobo, indicating that oxpeckers tended to select larger-sized hosts. This result is in agreement with five previous studies of yellow-billed oxpecker host selection that were re-analysed. At Matobo, yellow-billed oxpeckers per unit body surface area was highly and positively correlated with species-typical mass, meaning that oxpecker density on hosts increased with greater host mass. Analysis of host selection data from Stutterheim (1980) by Hart *et al.* (1990) also showed a positive relationship between the number of red-billed oxpeckers per unit body surface area and the species-typical mass of hosts. This relationship is likely due to larger hosts supporting higher densities of ticks (Olubayo *et al.*, 1993), and larger hosts supporting a higher proportion of adult ticks (Horak, 1982; Horak *et al.*, 1983).

There was a negative correlation between oxpecker host preference and mean herd size of ungulates in the wet season. As the number of oxpeckers per host or oxpecker density declined, oxpeckers were found on larger herds of smaller hosts. The preference for choosing larger-bodied host species (this study) coupled with the previously reported attraction of larger flocks of oxpeckers to larger herds of hosts (Mooring & Mundy, 1996) is the probable mechanism resulting in this correlation. As host body mass decreases, and with it host tick density and oxpecker foraging efficiency, it would be adaptive for oxpeckers to choose hosts in larger herds in order to decrease the distance to the next host animal once foraging efficiency on the current host falls below the cost-effective threshold.

As found in previous studies, oxpeckers selected hosts with short to medium-length hair. That hair length of hosts may play a role in oxpecker host selection was suggested by the finding that warthogs were more preferred as hosts than would be expected based upon their small size. This may be partly due to warthogs being sparsely haired, which would facilitate efficient search and removal of ticks by foraging oxpeckers.

Impala observed at Mpopoma Dam were more preferred hosts of oxpeckers than impala surveyed in other parts of the game park. Mpopoma was the only area surveyed in which impala hosts and water were consistently found together. Because oxpeckers require water to drink as well as to wash off blood from ticks that collect on their bills when feeding, water sources may be especially attractive to them. Impala hosts may have been attracted to Mpopoma more consistently and in higher densities than elsewhere, and aggregations at water points may be more visible to oxpeckers. Although it has been suggested that oxpeckers seen upon hosts at waterholes are using such hosts as platforms to gain access to water (Stutterheim, 1976), oxpeckers observed at Mpopoma Dam were actively foraging upon impala (Mooring & Mundy, 1996). Our findings are supported by Dale (1992b), who observed that impala found within 50 m of waterholes at Mana Pools National Park were more preferred hosts of oxpeckers than impala in woodland. Perhaps oxpeckers utilize any suitable host species found at preferred water sources.

We conclude that oxpecker host selection is influenced by an array of factors which impact the efficiency of foraging for ticks. The results of this study indicate that host body mass and tick availability are major factors impacting host preference, while host herd size, hair length and proximity to water may also play a role. Future studies can build on these insights by examining these and other factors in greater detail.

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