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Community ecology

The two oxpecker species reveal the role of movement rates and foraging intensity in species coexistence

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The two *Buphagus* oxpecker species are specialized passerines that forage for ticks and other food particles on the body of ungulates in the African savannahs. One of their intriguing features is their ability to coexist despite sharing the same, specialized diet. Using co-occurrence data (photographs of giraffes with oxpeckers on them) and approximate Bayesian computing, we demonstrate that yellow-billed oxpeckers changed host faster than red-billed oxpeckers and appeared to displace red-billed oxpeckers from preferred giraffe body parts. Conversely, red-billed oxpeckers exhibited a fuller use of each host and displaced yellow-billed oxpeckers from distal giraffe body parts. These findings highlight that the partition of giraffe hosts in two separate niches was only part of the coexistence story in this species pair. More precisely, the oxpeckers shared the resource by exploiting it at different rates. They engaged in different trade-offs between giving-up density, patch discovery rate and competitor displacement ability. They illustrate the importance of the time frame of interactions.

1. Introduction

The persistence of functional redundancies in ecosystems is key to understand biodiversity patterns [1–4]. For animals, variation in movement rates and foraging intensity may represent a somewhat under-studied way for otherwise incompatible species to coexist [5–8]. Species may share resources by exploiting them at different rates, for example, by trading the ability to discover new resource patches against the ability to displace competitors from them [5].

Oxpeckers (*Buphagus* sp.) are a pair of passerine species that exclusively feed on the ectoparasites, blood, exudates and exfoliates of ungulates in the African savannahs. Despite this extreme level of specialization on the same resource, they co-occur extensively in the same landscapes, and within landscapes, on the same individual mammalian hosts [9–15]. The only clear-cut difference between the niches of the two species is that the yellow-billed oxpecker (*Buphagus africanus*; hereafter YO) rarely visits smaller host species. However, morphological differences [16] suggest that the yellow-billed oxpecker may be able to displace the red-billed oxpecker (*Buphagus erythrorynchus*; RO) due to their larger size, while RO, due to its finer bill and smaller size, may have specialized on dexterity and flight at the expense of the ability to withstand interference by YO [10,12,14,17].

We analysed oxpecker co-occurrence in Hwange National Park, Zimbabwe, on giraffe *Giraffa camelopardalis*, which the above authors report as the preferred host species in southern Africa. We tested the hypothesis that the rate at which

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individual oxpeckers aggregate on giraffe hosts and leave them to find new ones differs between the two species and that it allows species coexistence. To do so, we interpreted the variation in oxpecker abundance across hosts as the transient dynamics of a two-species competition Lotka–Volterra equation [18], using approximate Bayesian computing (ABC). In particular, we quantified the differences in the flock size kinetics of the two species. We expected that, because it specialized on dexterity, RO would exhibit a fuller use of each giraffe, leading to slower flock size kinetics than YO. We complemented this exercise with a traditional approach to community composition analysis with metrics of dissimilarity and segregation (e.g. [19]), both at the level of individual giraffe hosts and within each giraffe, as a way to demonstrate that YO compensates for its relative lack of dexterity by the ability to displace RO from preferred locations.

2. Material and methods

(a) Data collection and preparation

Observers opportunistically photographed giraffes between 2007 and 2015 during the day from the network of tracks in the woodlands of the northeast of Hwange National Park, Zimbabwe (19°00′ S, 26°30′ E). We retained 345 pictures featuring the full left or right side of giraffes with oxpecker on them (42% had no oxpecker). R.G. marked down the oxpeckers with an estimated 99% detection rate (double observer protocol; [20]). G.P. identified the oxpeckers to species with an estimated rate of misidentification less than 2% (after a two-step process; electronic supplementary material, appendix S1). We only used pictures in which G.P. assessed that any bird in full view could have been identified given the distance and resolution of the photograph, thereby avoiding a bias towards adult oxpeckers and towards pictures with fewer identification challenges. We only recorded the birds on the exposed side of each giraffe, assuming that they were representative of the general pattern. The final sample size was 134 individual adult giraffes photographed between 09.00 and 17.00. Lastly, we located the oxpeckers on the bodies of the giraffes (abdomen, ano-genital area, back, rump, groin, head, lower leg, mane, neck, scapula, shoulder, tail, thigh or upper leg; see [20] for full details).

(b) Lotka–Volterra interpretation with approximate Bayesian computing

The two-species competition Lotka–Volterra equation (equation (2.1); [18]) describes the effect of intra- and interspecific density dependence on population fluctuations and community equiliriums [21]. Here, we tentatively used that equation to model the dynamics of emigration and immigration to and from a focal giraffe host. We considered the oxpecker counts on individual giraffes as samples from the transient behaviour of the Lotka–Volterra system

$$\begin{cases} \dfrac{dN_{RO}}{dt} = r_{RO}N_{RO}\dfrac{N_{RO} - K_{RO} - \alpha_{YO\to RO}N_{YO}}{K_{RO}} \\ \dfrac{dN_{YO}}{dt} = r_{YO}N_{YO}\dfrac{N_{YO} - K_{YO} - \alpha_{RO\to YO}N_{RO}}{K_{YO}} \end{cases} \quad (2.1)$$

The ‘population growth rates’ r_{RO} and r_{YO} represent the rate at which the species aggregate onto newly discovered hosts, i.e. the kinetics of the transient behaviour of the system before it reaches equilibrium. The ratio r_{YO}/r_{RO} quantifies how fast or slow YO is relative to RO. The ‘carrying capacities’ K_{RO} and K_{YO} represent the optimal number of oxpeckers per giraffe in the absence of the competitor. The ‘competition coefficients’ $\alpha_{RO\to YO}$ and $\alpha_{YO\to RO}$ represent the effect of competitor abundance on the decision to leave or stay. They quantify the niche overlap. The two species can coexist at equilibrium only if $K_{RO}/\alpha_{YO\to RO} \geq K_{YO}$ and $K_{YO}/\alpha_{RO\to YO} \geq K_{RO}$.

Equation (2.1) has more parameters than our data can support, but we devised an exploratory approximate Bayesian computation approach (with Monte Carlo Markov chain random walk and summary-based rejection criterion), denoted ABC [22]. In ABC, we compare the properties of simulated community compositions to those of the observed compositions (electronic supplementary material, appendix S2), in order to progressively exclude the simulation scenarios that are incompatible with our observations. More precisely, we compare the shape of the two-dimensional distribution in figure 1 (black dots) against that of simulations. As the algorithm progresses, only the most likely parameter values are selected, yielding the ‘posterior distribution’. If the data do not contain any information about a given parameter, the posterior distribution of that parameter will not differ from the prior that we specified at the start of the algorithm.

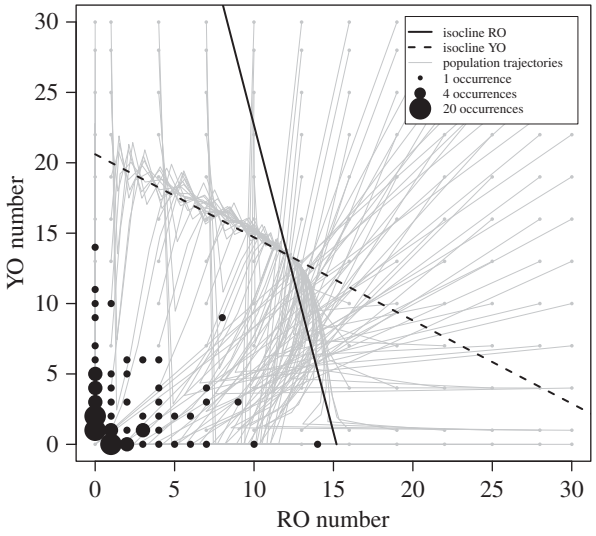


Figure 1. Number of red-billed (*B. erythrorhynchus*) and yellow-billed oxpeckers (*B. africanus*) on individual giraffe hosts in Hwange National Park, Zimbabwe. Black dots: field data. Each occurrence corresponds to one photographed giraffe individual. Diagonal lines: predicted species-specific isoclines of the Lotka–Volterra equation, i.e. the combinations of species abundances yielding a stable population for the focal species. Their intersection represents the attractive stable state of the two-species system, towards which the theoretical population trajectories (grey lines) converge.

(c) Segregation at the individual host level

To complement the inference from the ABC exercise, we computed three metrics of dissimilarity and segregation. D, the index of dissimilarity [23], corresponds to the proportion of individuals that would need to change host in order for the two species to have the same across host distribution. $E_{A\to B}$, the (asymmetric) index of exposure [23], corresponds to the probability that when an individual of species B meets another individual on the same host, that individual is of species A, and vice versa for $E_{B\to A}$. To test the null hypothesis that the two species did not influence each other, we performed a randomization test by permuting the association matrix. As a side note, additional metrics like the index of Freeman–Tuckey and the Kullback–Leibler distance were redundant with D and E, respectively, in our case.

(d) Segregation at the within-host level

First, we identified which body parts the two species were most often found on. We, hereafter, talk about 'preference' when the observed use was different from expectation under the uniform distribution across body parts, but most of the inference comes from comparisons between the two species. Then, we investigated whether the use of these body parts changed when the competitor was present or absent. Additionally, we *a priori* distinguished between distal (head, neck, mane, lower legs, thighs, flanks, groin, ano-genital area and tail) and central body parts (all the rest including the back, scapula and shoulders). Finally, we implemented the dissimilarity metrics at the body part scale.

3. Results

(a) Lotka–Volterra interpretation with approximate Bayesian computing

The growth rate of YO was 2.6 faster than that of RO (95% credible interval: 2.0–3.4). The transient dynamics played a larger role in explaining the species co-occurrence patterns than the predicted equilibrium state. Indeed, no oxpecker group appeared to even approach the predicted equilibrium size and composition (figure 1). The data, therefore, mostly contained information about the growth rates (electronic supplementary material, figure S3).

Across 826 posterior samples, 64% predicted that the species would coexist at equilibrium (average posterior scenario plotted in figure 1). Both competition coefficients were estimated below the prior median with a confidence interval that intersected zero (electronic supplementary material, figure S3), meaning that the niche overlap was perhaps not as strong as expected.

(b) Individual host level

The distributions of the two species across individual hosts were much more dissimilar than expected by chance ($D = 0.71$; randomization $p < 0.001$), indicating clear segregation at the individual host level (figure 1). The exposure of RO to YO was higher than the exposure of YO to RO ($E = 0.24$ versus 0.15, $p < 0.001$), meaning that when the two species co-occurred, RO was less abundant than when they occurred alone, and that the number of YO was easier to predict from the number of RO, than vice versa (figure 1; black dots). This is congruent with the expectation that YO can displace RO.

(c) Within-host level

Both species exhibited more similar distributions across the giraffe bodies than expected by chance ($D = 0.28$; $p < 0.001$). The oxpeckers both spent most of the time on the neck, mane, scapula and back (75% of RO occurrences and 58% of YO). However, RO used the neck much more than YO (31% versus 10%; χ^2-test, $p < 0.001$). YO were more frequent on the groin and ano-genital areas (11 versus 3%; $p = 0.005$) and on the back (15 versus 7%; $p = 0.01$). Overall, RO was found in distal parts 71% of the time, versus 57% for YO ($p = 0.002$).

RO use of distal body parts did not depend on whether YO were present (χ^2-test, $p > 0.5$), suggesting intrinsic preferences, but the frequency of RO decreased on the preferred body parts when YO were present (neck, mane, scapula and back; $p = 0.03$) and increased on the rest of the giraffes' bodies. YO use of central body parts also did not depend on whether RO were present ($p = 1$), but, by contrast, it did not decline on the preferred body parts in the presence of RO ($p = 1$). However, their distribution across distal body parts changed: more frequent on the legs when RO co-occurred (10 versus 3%; $p = 0.03$), less frequent in the ano-genital and groin areas (6 versus 14%; $p = 0.03$) and in the neck (3 versus 10%; $p = 0.03$). This suggested that YO dominated RO on the central body parts, the mane and the legs but were displaced by them in other distal body parts. Overall, RO were more likely to meet a YO than another RO on the same body part, but the reciprocal was not true ($E = 0.54$ versus 0.34).

4. Discussion

Traditionally, functional redundancies are explained either by fine-grained habitat selection [24,25], sometimes in a flexible manner depending on whether competitors are present [26–28], or by neutral interactions, i.e. heterospecifics do not represent more or less competition than conspecifics [2,3]. However, in the case of oxpeckers, previous studies provided mixed support for either of these explanations, and they rarely reported direct cohabitation on the same host other than giraffe hosts [9–15,29]. Koenig [12], in particular, recognized that traditional ecological models failed to explain the biogeography of the two oxpecker species because the differences in host species use and in within-host distribution did not differ in sympatry or in allopatry.

We offer a new hypothesis to explain the patterns of co-occurrence of oxpeckers on giraffe hosts, namely the ability to partition resources *within* rather than *across* host species, via key differences in movement rates and foraging intensity. In other words, the two oxpecker species can coexist by exploiting the same resource but at different rates. These findings confirm the role of the time frame of species interactions [30] and validate the vision of Koenig [12] that oxpecker flocks are in a permanent state of disequilibrium. Here, we further detail how these dynamics seem to happen by way of species-specificity in the extinction and colonization processes. In this new interpretation, we would explain the restricted geographical distribution of RO, the more 'intense' forager, by the fact that dense populations of ungulates are needed to allow YO to express its low-intensity foraging behaviour, and therefore that without dense ungulate populations RO is excluded by YO.

The differences in flock size kinetics and foraging tactics are fully congruent with, first, the morphological differences between the two species, which suggest that RO is more dexterous than YO, but YO is able to displace it. YO was, in particular, expected to interfere with RO by preventing them from roosting on the giraffe hosts [10,29]. Although we only documented daytime behaviour, we did find YO more often than RO on body parts that are used for roosting: back, (inner) upper legs and groin. Second, our findings are congruent with differences in plumage: the plumage of YO is more contrasting than that of RO, suggesting more opportunities for public information use and fast aggregation [31]. The faster kinetics of YO combined with the way they distributed themselves on the giraffe hosts suggest a tactic of exploiting the most accessible resource and leaving before having consumed all of the giraffe's parasites. This would indicate that at least YO

behaves perhaps more like a commensal than a mutualistic partner because they may not influence the attachment duration of ticks that are attached on the more distal body parts.

Our findings are overall completely compatible with the hypothesis of a multi-way trade-off between giving-up resource density, ability to displace competitors and the rate at which new patches are discovered [5]. In summary, the emerging community properties resulted from a collection of transitory dynamics on each individual giraffe, with species-specific local flock size kinetics deriving from contrasting foraging tactics. More than the ability to coexist at equilibrium on each separate giraffe, what promoted coexistence among the two oxpecker species was the movement rates.

This notion helps interpret a broad range of previous findings in other avian guilds. For example, among the Australian parrots, wide-ranging species explore their local environment less intensively than species with small home ranges [32], like YO forages less intensively but switches host faster than RO. In *Aythya* ducks, females of different species make different trade-offs between parasitizing conspecific nests and laying in their own nest, which means they fine-tune how spatially and temporally spread out their investment is [33,34]. In mixed-species flocks of insectivorous passerines, where many species share the same prey base, some species employ fast-paced foraging techniques aimed at flushing a maximum of prey, while others employ slow-paced techniques leaning on visual detection of motionless prey [35].

As a final side note about the conservation relevance of our findings, YO, but not RO, declines strongly after the host megafauna is removed, even when smaller hosts are conserved, and the megafauna is replaced by cattle [17,36–38]. The post-defaunation decline in YO is so far only reported in the parts of its range where it co-occurs with RO, namely southern and eastern Africa. Therefore, competition with the more dexterous RO might play a role in the post-defaunation decline in YO [17]. We speculated above that YO should dominate at low densities of large hosts, but now those hosts are almost extinct. Alternatively, the reliance on public information might prove maladaptive when foraging on small and healthy hosts [11].

Data accessibility. Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.jsxksn04x [39].

Authors' contributions. All authors agree to be held accountable for the content therein and approve the final version of the manuscript. G.P. designed the study, performed the statistical analysis and wrote the first draft. G.P., C.B. and R.G. prepared the data. C.M. and C.B. facilitated data acquisition. G.P., C.B., R.G. and C.M. edited the next drafts.

Competing interests. We declare we have no competing interests.

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