

Current Biology

Oxpeckers Help Rhinos Evade Humans

Highlights

- Field experiments to test whether oxpeckers helped rhinos detect and evade humans
- Oxpeckers enabled around 40%–50% of rhinos to evade humans undetected
- After oxpecker calls, alert rhinos faced humans' favored hunting direction: downwind
- Anti-predator eavesdropping occurs among non-vocal, asocial species, too

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In Brief

Predation threat alone, not sociality, might be the main driver of eavesdropping behavior between animal species, but remains difficult to test *in situ*. Plotz and Linklater show experimentally that black rhino, a solitary, non-vocal species vulnerable to human predation, use oxpecker alarm calls to better detect and avoid humans.



Oxpeckers Help Rhinos Evade Humans

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SUMMARY

Evolutionary theory expects social, communicative species to eavesdrop most on other species' alarm calls [e.g., 1, 2] but also that solitary-living species benefit most from eavesdropping [3, 4]. Examples of solitary species responding to the alarm calls of other species, however, are limited and unconvincing [3–5]. The Swahili name for the red-billed oxpecker (*Buphagus erythrorhynchus*) is *Askari wa kifarua*, the rhinos' guard [6]. Black rhino (*Diceros bicornis*) are a solitary-living, non-vocal species and are critically endangered through hunting. We searched Hluhluwe-iMfolozi Park, South Africa, for rhinoceros for 27 months with and without the aid of radio telemetry and conducted 86 experimental, unconcealed approaches to 11 rhino, without or with varying numbers of resident oxpecker. Oxpeckers enabled rhinos to evade detection by us in 40% to 50% of encounters. Alarm-calling by oxpeckers significantly improved the rate and distance that rhinos detected our approach from 23% to 100% and 27 ± 6 m to 61 ± 4 m, respectively. Every additional oxpecker improved detection distance by 9 m. Rhinos alerted by oxpeckers' alarm calls never re-oriented in our direction but moved to face downwind. Thus, oxpeckers' calls communicate only threat proximity, not direction, and rhinos assume the hunter is stalking from downwind. We confirm that oxpeckers guard rhinos and the importance of depredation, not sociality, in the evolution of eavesdropping [4, 7]. Conservationists should consider reintroducing oxpeckers to rhino populations, reinstating their anti-human sentinel [8].

RESULTS

Rhinos Avoiding People

Twenty-seven adult male and 24 adult female rhinos found on 100 occasions without the aid of radio telemetry were similarly

likely to have oxpeckers (9 of 27 male and 8 of 24 female rhino encounters: $\chi^2_1 = 0.21$, $p > 0.1$) and had similar numbers of oxpeckers when they were resident (oxpecker group size, average \pm 1SE: male 3.4 ± 0.56 , female 4.0 ± 0.50 ; Mann-Whitney $U = 25$, $p > 0.1$). The 51 rhinos found without the aid of radio telemetry were significantly less likely to have oxpeckers than the 14 adult females found using radio telemetry (untagged: 17 of 100 detections; cf. tagged: 56 of 100 detections; $\chi^2_1 = 34.3$, $p < 0.00001$). The observed differences in oxpecker residency between the two types of rhinos found (i.e., with and without radio transmitters), was then used to calculate the number of untagged rhinos with oxpeckers that evaded us for given numbers of rhinos encountered using Equation 1 (STAR Methods). By inputting the different possible numbers of rhinos present but undetected (R_u), the number of encounters with untagged rhinos with resident oxpeckers that went undetected (R_{uo}) can be estimated (Equation 1, see STAR Methods), e.g.,

$$\text{if } R_u = 0 (\text{i.e., no rhino evaded us}), ((100 + R_u) \times 0.56) - 17 = 39(R_{uo})$$

Then, we calculated their contribution as a percentage ($\%R_{uo}$) of the total number of rhinos encountered (i.e., $(39/(100+0)) \times 100 = 39\%$) (Figure 1). As expected, the $\%R_{uo}$ asymptotes toward 56% (the proportion of oxpeckers present on rhinos with horn implant transmitters) where R_u is large, i.e., ≥ 400 , because 20% or fewer of all rhino, i.e., $(R_u/(R_d + R_u)) \times 100 = 100/500$, are assumed to have been detected. Calculations indicate that if our detection rate was poor (i.e., 33%–25% such that R_u ranged from 200 to 300), then we failed to detect rhinos in ~ 150 –200 encounters or over 50% of encounters because they had resident oxpeckers. But, if we were successful at detecting over half to 80% of all rhinos encountered (i.e., R_u ranges from 100 to 25), then we failed to detect rhinos on ~ 50 –100 encounters or in $\sim 42\%$ – 47% ($\%R_{uo}$) of encounters because they had resident oxpeckers. Assuming the highest overall detection rates possible (i.e., approaching 100% or an R_u near 0) indicates that the number of times rhinos went undetected because they had resident oxpeckers cannot have been fewer than 70 occasions or 40% of encounters (Figure 1).

Compared with untagged rhino (median of 1 sighting per individual), individual tagged rhinos were less evenly sighted



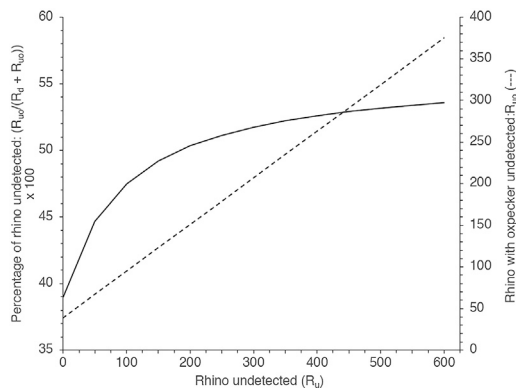


Figure 1. Rhino Avoiding People

The estimated proportion (line and left axis) and number (dashed line and right axis) of potential untagged rhino encounters that were prevented by resident oxpeckers on rhinos, given hypothetical numbers of occasions that rhinos evaded us (R_u) during our activities in the study area to generate 100 rhino encounters (R_d ; such that $R_u + R_d =$ the total number of encounters possible).

because horn-implant radio transmitters were inserted at different times over the 27-month project. Nonetheless, using a larger dataset available to us (including 86 initial sightings of rhinos with and without oxpeckers prior to experimental approaches—see next section), analysis shows the presence of oxpeckers on tagged rhinos consistently remained above 50% (e.g., 94 out of 186 sightings) and was, thus, representative of oxpecker presence on the wider rhino population (see rhinos avoiding people raw data in the [Key Resources Table](#)).

Human Approach Trials

Oxpeckers significantly improved rhinos' human approach-detection rate (Fisher's Exact Test, $n = 86$, $p < 0.00001$). Black rhinos without oxpeckers detected 23% (11 of 48) of approaches at an average 27 ± 6 m (1SE; range 8–74 m) (Figure 2A). They appeared to detect our approach acoustically ($n = 5$) (e.g., noise from footfall or walking through grass) or olfactorily ($n = 6$) (e.g., via eddies or temporary shifts in wind direction). The 37 undetected approaches were terminated at an average 21 ± 2 m (range 5–39 m). But when oxpeckers were resident, rhinos detected all (38) our approaches at an average 61 ± 4 m (range 20–110 m) (Figure 2A). On all occasions, oxpeckers alarm-called immediately before the rhinos detected our approach. All rhinos responded to oxpecker alarm calls by becoming vigilant—standing alert from resting in a lying ($n = 17$ of 38, 46%) or standing ($n = 12$ of 38, 32%) posture, feeding or drinking ($n = 7$ of 38, 19%), or walking ($n = 1$ of 38, 3%).

A significant positive relationship between oxpecker number and detection distance was found ($R^2 = 0.59$; $F_{8, 85} = 11.5$, $p < 0.001$) (Figure 2B). Random effects for rhino identity did not contribute additively or interactively to the relationship (additive: $F_{9, 85} = 0.33$, $p = 0.96$; interaction: $F_{21, 85} = 0.77$, $p = 0.73$).

When first sighted and before our approach, black rhinos with and without oxpeckers were not orientated differently with respect to wind direction (χ^2_2 N, $86 = 3.02$, $p = 0.22$) (Figure 2C). The distribution of orientations with respect to wind by rhinos without oxpeckers did not significantly change when they were

approached, even though 23% of our approaches were detected by the rhino (χ^2_2 N, $85 = 2.23$, $p = 0.33$) (Figure 2C). Black rhinos were significantly more likely to orientate downwind (i.e., 36 of 38 approaches, 95%) after an oxpecker alarm call, rather than crosswind ($n = 1$, 2.5%) or upwind ($n = 1$, 2.5%) (χ^2_2 N, $76 = 34.94$, $p < 0.00001$) (Figure 2C). Rhino never turned to face the person approaching crosswind. After becoming alert, rhinos either ran upwind to leave our view (9 of 38 approaches, 24%); walked downwind (10 of 38, 26%), apparently to investigate; or maintained a vigilant standing posture (19 of 38, 50%), at least until we moved out of visual contact with them.

DISCUSSION

Our experiment confirms hunters' anecdotes and folklore that red-billed oxpeckers are black rhinos' anti-human sentinels. Oxpeckers enabled rhinos to evade detection by people and initiate anti-predator behaviors when they were found.

Oxpeckers called as we approached (Audio S1), and rhinos always responded immediately by becoming vigilant [11]. Oxpeckers' alarm-calling enabled a greater than 4-fold increase in the human detection rate for rhinos without oxpeckers. Without oxpeckers, we were able to approach rhinos undetected in over three-quarters of attempts. Moreover, oxpeckers' calling more than doubled the distance at which rhinos detected our approach. Every additional oxpecker increased average detection distance by 9 m.

Improved detection rate and distance estimates are conservative because, without the aid of horn-implant transmitters and radio telemetry, we were much less successful at detecting the rhinos we encountered if they had resident oxpeckers. Oxpeckers enabled rhinos to evade us and remain undetected. We estimate that rhinos with oxpeckers eluded us on at least 70 occasions and in over 40% of rhino encounters during our movements in the reserve. The true number and proportion of encounters that went undetected because of oxpeckers could have been much higher, i.e., up to 300 and 52%. It seems improbable, however, that the number and proportion exceeds this amount because we saw only 51 different rhino over 27 months in the approximately 320 km² area of the park where we worked (i.e., ~ 0.16 rhino per km²), consistent with density estimates in others (e.g., 0.11 rhino per km² in Kruger National Park) [12].

The anti-predator response of rhinos to oxpecker alarm calls is also revealing. Rhino almost always (95% of occasions) re-orientated to direct their vigilance downwind and never at the approaching person. Thus, oxpecker alarm calls do not include information about the direction of the threat, only its proximity, and rhinos continuously evaluated wind direction to know the direction of their sensory "blind-spot" and greatest vulnerability. Hearing an oxpecker's alarm call, rhinos almost always assumed they were being stalked from downwind.

Our results raise three interesting questions about rhinos' relationship with oxpeckers. First, are rhino populations sympatric with oxpeckers less vulnerable to human hunting? Second, are oxpeckers' alarm calls specifically anti-human signals, or do they warn of other predators too? Lastly, are the rhinos just eavesdropping on oxpecker-oxpecker alarm calls or are their calls a cooperative signal to rhino?

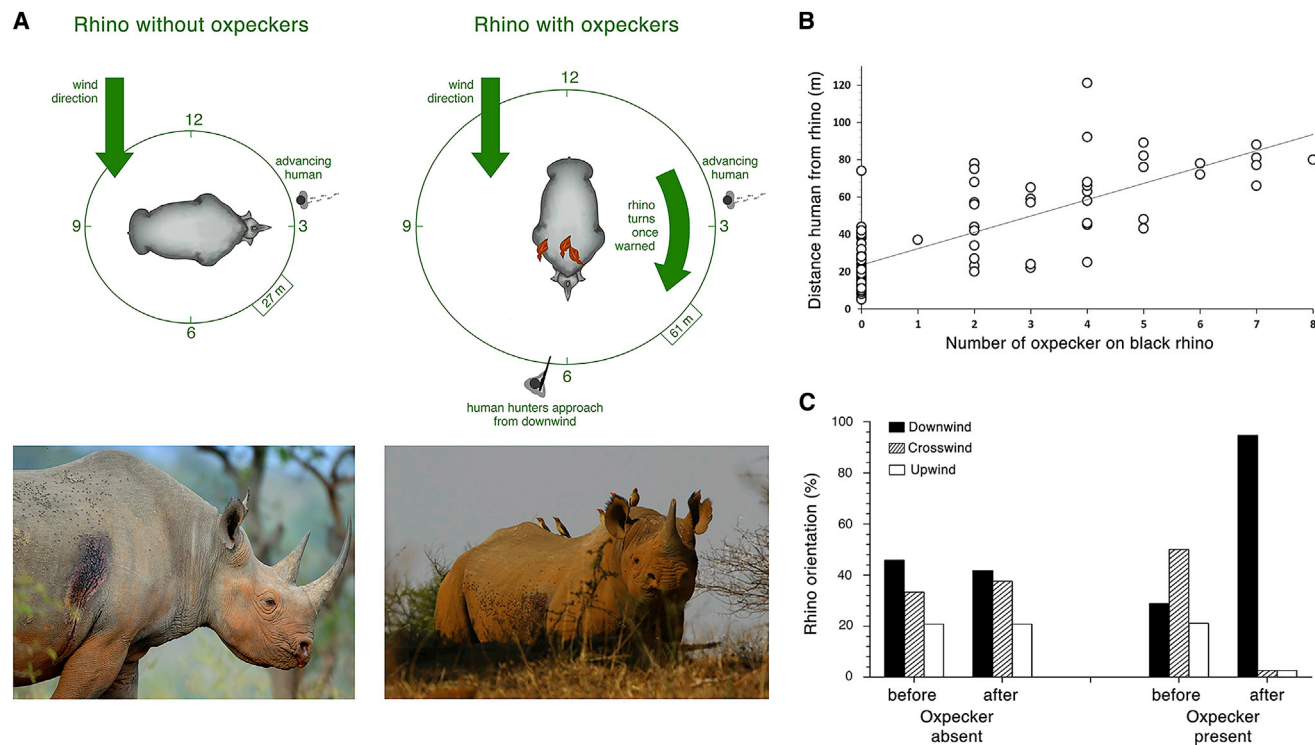


Figure 2. Human Approach Trials

(A) Schematic using an analog clock to describe direction of human-rhino approach trials with and without oxpeckers. An observer (human “threat”), walked from the location downwind around the rhino to approach it from 3 or 9 o’clock and record, with a laser Rangefinder, how close they could get before being detected. The orientations selected by rhinos relative to wind (i.e., upwind = 11 to 1 o’clock, crosswind = 8 to 10 and 2 to 4 o’clock, and downwind = 5 to 7 o’clock), and human approach direction was also determined, before (i.e., at first sighting of rhino) during, and at the completion of the approaches (see also Figure 2C). We show experimentally that: rhinos without oxpeckers (left) detected and orientated in the direction of the approaching person on 23% of approaches (11 out of 48), at a distance of about 27 m. Rhinos with oxpeckers (right) always detected the approaching person (100%, 38 out of 38) at a distance of about 61 m, where rhinos turned to face downwind—the direction of approaching hunters (see also Figure 2C), when oxpeckers were present to give the alarm (see also Audio S1). Schematic adapted with permission from [9]. Photographs by Dale Morris (left) and Jed Bird (right).

(B) The relationship between the number of oxpeckers resident on black rhinos and the distance the approaching human threat was detected by rhinos (detection distance = $8.98(\text{oxpecker group size}) + 23.47$, $R^2 = 0.59$: GLM repeated-measures ANOVA, $F = 8.47 = 11.5$, $p = 0.01$ see also Figure 2A).

(C) The direction rhinos faced relative to wind direction (up-, cross-, or down-wind) before (at first sighting) and after an experimental approach by a person from crosswind when oxpeckers were absent ($n = 48$) or present ($n = 38$) on the approached rhino (see also Figure 2A and [10]).

Oxpeckers Saving Rhino?

Earlier detection prevents hunters from getting closer. Improvements in detection distance provided by oxpeckers might seem small but marksmanship errors multiply with increasing distance [13, 14]. A projectile’s 1% directional error (from 45 degrees) lands 0.7 m from target center at 30 m and 1.3 m at 60 m. Greater distance also makes compensating for projectile ballistics and wind more difficult and increases the likelihood objects (e.g., vegetation) will interrupt hunters’ aim or ricochet, slowing or stopping the projectile [14, 15]. Earlier detection also reduces the time for hunters to aim and causes the animal target to move, affecting hunters’ success [13]. Oxpecker alarm-calling probably reduces hunters’ success, especially when the improvements in detection distance is combined with our observation that oxpeckers enabled rhinos to avoid us undetected approximately half of all occasions that we were near. Whether these would be enough to retard population decline from illegal hunting remains to be demonstrated. Hunting (non-lethal) experiments

or comparisons across populations with and without oxpeckers and with known or equal hunting pressure will be needed to prove the fitness benefit.

Anti-predator or Anti-human?

Adult mega-herbivores are vulnerable to human hunters but mostly immune to other predators [16, 17]. And, rhinos’ anti-predator behavior and weaponry (e.g., size and horns) is effective against large carnivores like spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*) [16]. It is, however, much less effective against organized groups of humans and their projectile weapons who have successfully hunted rhinos with spears since the late Pleistocene (i.e., < 50,000 years ago) [17, 18] and, with modern weaponry, to the brink of extinction. Human overkill reduced rhinos from ~700,000 in 1850 to ~2,400 by 1995 [19], imposing an extreme selective pressure on rhinos and oxpeckers who favor feeding on them. Thus, oxpeckers’ alarm-calling could be a peculiarly anti-human behavior and of comparatively recent origin.

Black rhinos run from people and their scent, but not nearly as much from other large predators [16, 17]. And, the assumption by rhinos that oxpeckers' alarm-calls indicate a predator threat downwind also matches a human hunter's propensity to hunt from that direction for a 6-fold increase in hunting success [13, 20]. Other large predators do not hunt from downwind [21] but depend more on the proximity of cover or scattering and dis-orienting prey toward others waiting in ambush. There are also not yet any reports of oxpeckers alarm-calling in response to non-human predators. All these contribute circumstantial evidence for oxpecker alarm calls being recent and specifically anti-human signals to rhino. Nonetheless, observations of the behavior of oxpeckers and rhinos being hunted by other predators is needed.

Rhino Eavesdropping or Oxpecker Mutualism?

After an alarm call, oxpeckers move to congregate along the host's spine from more vulnerable feeding positions over the rhino's flanks, underside, and legs. Thus, they might alarm-call to warn each other that, because of an approaching person, their host is about to move. If that is true, then rhinos are simply eavesdropping on oxpecker conspecific signals [e.g., 22]. However, under extreme hunter-imposed selection, eavesdropping might have exapted into cooperative calling. Oxpeckers that called preserved their favored host and food resource.

That oxpeckers not only feed on rhinos' ectoparasites, but particularly like to also feed from the large and permanent open lesions on rhinos' flanks, caused by the filarial parasite *Stephanofilaria dinniki* [10], improves the likelihood of alarm-calling becoming cooperative. Thus, oxpeckers can be both mutualists and parasites on rhinos. The oxpecker-rhino relationship is sometimes a conditional mutualism [23–25]. Where costly wound-feeding parasitism by oxpeckers occurs, they might trade sentinel behavior for it [26] to explain why rhino tolerate wound-feeding by oxpecker [10], whereas other ungulates do not (e.g., African buffalo, *Syncerus caffer*) [23, 27]. The hypothesis that oxpeckers alarm-call for rhinos when they are feeding parasitically is intriguing but still needs to be tested [10]. If true, populations of black rhinos without filarial lesions, being outside the nematode parasite's biogeographic range [10], should not alarm-call for rhinos or do it much less.

CONCLUSIONS AND IMPLICATIONS

Our evidence confirms the appropriateness of red-billed oxpeckers traditional name, *Askari wa kifaru*—the rhino's guard [6, 10]. Oxpecker populations have, like rhinos', also declined and became locally extinct in many places, primarily because they were poisoned by the anti-ectoparasite dips used in cattle farming [10]. Thus, most rhino populations now exist without them. Conservationists might consider re-introducing oxpeckers to rhino populations [28] or re-introducing the two species simultaneously to wildlife reserves to reinstate a proven anti-human sentinel for rhino. Both are conservation-reliant biodiversity [10, 29] and oxpeckers might help improve rhino survival where park security fails to deter or detect illegal hunting [8]. Lastly, our field experiment confirms that a solitary-living species without a complex and frequently used

vocal repertoire, like rhinos, do eavesdrop on the alarm calls of another species to detect and evade a predator. It is the vulnerability of black rhinos to a human predator that appears to have driven its inter-specific associative learning and adaptation [e.g., 30]. Vulnerability alone, without recourse to sociality and a communication repertoire, appears to be enough for the evolution of eavesdropping.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2020.03.015>.

A video abstract is available at <https://doi.org/10.1016/j.cub.2020.03.015#mmc2>.

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AUTHOR CONTRIBUTIONS

R.D.P. and W.L.L. conceived the project, and both contributed to experimental design, interpretation, statistical analyses, and writing. R.D.P. carried out the fieldwork, including tracking rhinos and preparing and performing the experimental approach trials.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|--|---------------|---|
| Deposited Data | | |
| Calculations of undetected untagged rhino that avoided us< | Mendeley Data | http://dx.doi.org/10.17632/xkwjwvst66.1 |
| Rhino Avoiding People Raw Data | Mendeley Data | http://dx.doi.org/10.17632/gx8xv3nc7f.1 |
| Human Approach Trials Raw Data | Mendeley Data | http://dx.doi.org/10.17632/55ynhvhv7sp.1 |
| Software and Algorithms | | |
| IBM SPSS Statistics 25 | [31] | https://www.ibm.com/support/pages/downloading-ibm-spss-statistics-25 |

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information should be directed to and will be fulfilled by the Lead Contact, Dr Roan Plotz (roan.plotz@vu.edu.au). This study did not create newly generated materials or reagents.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

In this field experiment we studied interactions between wild populations of black rhino (*Diceros bicornis*) and the red-billed oxpecker (*Buphagus erythrorhynchus*) in Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa. The 200–300 black rhino (*D. b. var. minor*) of Hluhluwe-iMfolozi Park are descended from the largest population in South Africa (of just two) to survive the 20th Century's human over-kill. They are still hunted [32] and live with red-billed oxpecker (Buphagidae) [10, 33, 34]. Almost all rhino in the population were individually identifiable from unique combinations of ear notches made at their capture [32]. As part of wider research project [10, 11, 35], fourteen adult female rhino were between January 2006 to October 2008, intermittently chemically immobilized by a wild-life veterinarian darting from a helicopter and a radio transmitter installed in their horns [36].

METHOD DETAILS

Rhino avoiding people

Searching for rhino, with (tagged) and without (untagged) horn implant radio transmitters over 27 months and recording the number of oxpecker resident on each rhino allowed us to test whether oxpecker improved rhinos' ability to detect and avoid humans. We recorded the number of oxpecker seen on untagged rhino without radio transmitters found 100 times during our searches and other research activities within the population's range [10, 11, 35], to compare with the oxpecker seen on the 14 tagged rhino with radio transmitters that were found using radio telemetry on 100 occasions (see next section) over the same period: April 2007 to July 2009. Radio transmitters enabled us to approach and sight tagged rhino without first being detected. If oxpecker were acting as anti-human sentinels for rhino, we predicted that tagged rhino we found and approached undetected using radio telemetry will be more likely to have resident oxpecker than the untagged rhino we detected without the aid of a radio signal. And because untagged rhino without radio transmitters ought to be more detectable when oxpeckers were absent, we expected oxpecker residency on the tagged rhino found using radio telemetry to therefore be more representative of the rate of oxpecker residency on the larger rhino population. The difference in oxpecker residency between the two types of rhino found (i.e., with and without radio transmitters), was then used to calculate the number of untagged rhino with oxpeckers (and without a horn implant transmitter) that avoided us for given numbers of rhino encountered by developing and using an equation (see Equation 1 in quantification and statistical analysis).

Human approach trials

The ability of rhino to eavesdrop on oxpecker alarm calls and improve their detection and avoidance of human hunters is an untested hypothesis. Eighty-six experimental human approaches to 11 tagged rhino allowed us to test whether (1) our approach coincided with oxpecker alarm calling and anti-predator behavior by black rhino, (2) oxpecker alarm calls signaled the direction of our approach, and (3) oxpecker, and increasing numbers of oxpecker, improved black rhinos' human-detection rates and distance.

Rhino were selected in random sequence and found using radio telemetry because it enabled us to find them undetected from downwind (i.e., leeward; [10, 34]). Once sighted, we recorded date and time, wind direction, and rhino identity and orientation. Orientations were described as the anterior side of an imaginary line drawn through the pectoral girdle (shoulder to shoulder). Wind

directions and orientations were recorded by imagining the 12 h of an analog clock encircling the rhino with the stationary observer always at 6 o'clock (Figure 2A). Lastly, the number of oxpeckers perching and feeding on the rhino was recorded.

Each approach had the following sequence: (1) one observer with a telescope (Bushnell Trophy Xtreme spotting scope 20–60 × 65) remained stationary at a concealed position (i.e., 6 o'clock) near where we first sighted the rhino and downwind of its location and recorded oxpecker number and their, and the rhino's, pre-alert behavior. (2) The second observer walked in a wide arc to the left or right until they reached a location approximately perpendicular and crosswind of the first observer-rhino axis (i.e., at 3 or 9 o'clock). (3) From there they walked at constant speed in a straight line toward the rhino. (4) If, during the approach, the rhino became alert, the suspected reason (e.g., oxpecker alarm call or observer noise or scent) and the rhino's post-alert orientation was recorded by the stationary observer. (5) The approaching observer recorded the nearest distance they attained before the rhino became alert or further approach was unsafe, but they remained undetected. Typically, approaches were recorded as undetected when it was unsafe for the observer to move closer to the rhino. The proximity of the rhino (typically < 20 m) but lack of suitable refuge for the observer (e.g., climbing tree) made advancing closer too dangerous. Distances to rhino were measured using a laser Rangefinder (Leica PINMASTER II).

So that our approaches were unconcealed and observations uninterrupted, we only carried out trials in open habitat that was typically short to medium height grassland and savannah. If during approaches: the stationary or approaching observer could not maintain visual contact with the rhino, the distance to the observer became too large to hear oxpecker alarm calls, or oxpeckers flew onto or off the rhino such that they could have had an aerial view of the approaching human, or the rhino was already alert prior to commencement (e.g., stand-alert posture) [11], including alerted by oxpeckers that had already alarm-called (e.g., described as a *Krsss* sound) [37] (Audio S1); the approach was abandoned and data not used for analyses ($n = 22$). Between May 2008 and June 2009, 86 unconcealed human approaches to rhino were completed and 38 were to rhino with resident oxpecker.

QUANTIFICATION AND STATISTICAL ANALYSIS

Rhino avoiding people

The difference in oxpecker residency between the two types of rhino found (i.e., with and without radio transmitters), was used to calculate the number of untagged rhino with oxpeckers (and without a horn implant transmitter) that avoided us for given numbers of rhino encountered using the following equation:

$$(R_d + R_u) \times O = R_{do} + R_{uo} \quad (\text{Equation 1})$$

where R_d = Occasions untagged rhino present and detected (seen by us) i.e., 100, and

R_u = Occasions untagged rhino present but undetected (value unknown), such that $R_d + R_u$ = all untagged rhino present that could have been detected by us.

And, O = proportion of occasions with oxpecker present on tagged rhino (from rhino with horn implant radio transmitters found using VHF radio telemetry), such that

$(R_d + R_u) \times O$ = the number of all untagged rhino encountered that had oxpecker.

Lastly, R_{do} = number of occasions untagged rhino detected (seen) with oxpecker, and

R_{uo} = number of untagged rhino that were present but undetected because they had oxpecker.

The equation can be rearranged to calculate R_{uo} given different, proposed values of the unknown R_u (Figure 1).

Human approach trials

Focusing on female adult black rhino that were fitted with horn implant radio transmitters ($n = 11$), we compared the observed difference in responses by black rhino, with and without oxpeckers present, to 86 human approaches. Fisher's Exact test was used to analyze the difference in the detection rates between the two groups.

We used a GLM Repeated-measures ANOVA for analyzing rhino's detection distance (Log transformed) of human approaches with varying numbers of oxpeckers. Chi-square comparisons were made of black rhino's orientations with and without oxpecker present at first sighting, during approaches and after oxpecker alarm calls. For all analysis statistical significance was considered at $p < 0.05$.

DATA AND CODE AVAILABILITY

All original data are available by contacting first author, Dr Roan Plotz (roan.plotz@vu.edu.au); for data on calculations of undetected rhino that avoided us, see: <http://dx.doi.org/10.17632/xkwjwvst66.1>, for rhino avoiding people raw data see: <http://dx.doi.org/10.17632/gx8xv3nc7f.1>, and for human approach trials raw data see: <http://dx.doi.org/10.17632/55ynhhv7sp.1>.