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Short communication

The effect of infrastructure on the invasion of a generalist predator: Pied crows in southern Africa as a case-study

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A B S T R A C T

Corridors can favour range expansion of generalists. Specifically, roads have been suspected of facilitating invasion. In southern Africa, pied crows (*Corvus alba*) have either colonised or increased in abundance, perhaps because climate warming has shifted their available habitat, assisted by roads. We investigated the link between abundance of this generalist bird species and roadkill, taking into account whether road infrastructure, socio-economics and driving habits influence roadkill. We surveyed 1170 km of principal roads in South Africa (SA), Botswana, and Zimbabwe. SA has the most complex economy incorporating good roads, fast vehicles and more human activity. The economy of Botswana is intermediate and Zimbabwe's is smallest. Crows were sighted nearly 10 times more often in SA than Zimbabwe, although crows were historically rare in 60% of the SA area we surveyed. They were five times more abundant in Botswana than Zimbabwe. Roadkill was 20 times more frequent in SA and eight times more frequent in Botswana, than Zimbabwe. The average number of vehicle occupants in Zimbabwean vehicles was 5.5 and 2.8 times that of SA and Botswana, respectively. That is, the number people transported per roadkill was 4.5 in South Africa, compared to 433 in Zimbabwe. There was an interaction between roadkill and country. SA had the greatest increase in crow numbers per roadkill, indicating that crow densities were greater in SA because roads are particularly important for crows compared to the surrounding environment, and/or that the regular supply of roadkill on South African roads builds a "reservoir" of crows. Increased crow abundance places additional predation pressure on mammals, reptiles, birds and insects in the surrounding scrub-vegetation. Telegraph poles contribute to the problem, providing nest sites in an environment that provides few other nests and perches. An approach to socioeconomic development that considers contributing factors can be expected to reduce the spread of opportunist species.

1. Introduction

The emerging economies in Africa, Asia and South America (representing six of the world's 7.3 billion people) continue to urbanize and industrialize at unprecedented rates, leading to a proliferation in road networks (Hulme, 2009; Population Reference Bureau, 2013). Roads can facilitate introduction of alien invasive species, and range expansions of indigenous species, most notably generalists, into range-contiguous areas where they did not previously occur (Marzluff and Neatherlin, 2006; I-Ching et al., 2011). Roads also impact small vertebrate diversity through habitat loss, increased human activities, and death by collision (Trombulak and Frissell, 2000), lowering abundance and diversity (Huijser and Bergers, 2000), and enhancing the probability of extinctions (Row et al., 2007). Reviews and meta-analyses concur that roads have negative impacts on animal abundance and distribution (Fahring and Rytwinski, 2009; Benítez-López et al., 2010). Some species, e.g. raptors, can benefit from roadkill, however, and it is estimated that 60–90% of roadkill is scavenged within 36 h (Antworth et al., 2005. Lambertucci et al., 2009).

To better understand the impact of this global proliferation in roads, and whether degree of development impacts invasion, we conducted a case study spanning three contiguous African countries with road networks at differing stages of development. Quantifying the spread of invasive species requires accurate baseline data and monitoring over time. The Southern African Bird Atlas Project (SABAP, 2016) of 1987–1993 and 2007–2016 records presence of birds in grid cells from multiple observer visits, spans 3 decades, and informs of observation rates and range shifts in individual species across the countries studied. In the Karoo and Fynbos systems of southern Africa, reported sightings of pied crows (*Corvus albus*), omnivorous generalists, have doubled over

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20 years (Cunningham et al., 2015), and the range has extended into one of the world's 'hottest' biodiversity hotspots. For Botswana and Zimbabwe, ranges have remained constant.

The pied crow diet is broad, including small mammals, amphibians, reptiles, fledglings and eggs, in addition to plant matter (Hockey et al. 2005). The impact of invasion on a nutrient-poor food web is likely to be complex (Sax et al., 2005). For example, rates of passerine nest predation may increase, but could be balanced by pied crows' predilection for other nest predators such as snakes and small mammals. Prominent governmental, non-governmental, and research organisations warn of negative impacts to diversity, including trophic cascades (Cunningham et al., 2015). Pied crows have been observed to prey heavily on range-restricted angulate tortoises (*Chersina angulate*; Fincham and Lambrechts, 2014, SCARCE, 2007). The high herpetological diversity (Tolley et al., 2009) and endemism of amphibians (Seymour et al., 2001) in the Fynbos make increased abundance of a generalist predator problematic. Furthermore, diversity of reptiles in the Karoo extent of this study area may be underestimated, owing to low sampling effort in that region (see, e.g. Tolley et al., 2016).

Climate warming may increase habitat for pied crows, and roads are possible conduits for range expansion (Siegfried, 1963; Dean and Milton, 2003; Cunningham et al., 2015). Pied crows make considerable use of road kill in their diets, and infrastructure along roads (e.g. telegraph poles) are particularly important as perching and nesting sites (Dean et al., 2006). How roads and socio-economic factors interact to facilitate this expansion remains unexplored. We tested for the first time the association between pied crow abundance, roadkill, socio-economics and human activity in rural areas. We surveyed roads in three countries (South Africa [SA], Botswana and Zimbabwe) with differing socio-economic conditions and rural land occupancy levels, that share a contiguous pied crow population. Changes in species distributions may be better understood through a lens that includes local socio-economic considerations, in addition to global phenomena like climate change. We hypothesised that pied crows increase in abundance as scavenging opportunities (roadkill and human activity) increase. To confirm the link and explore underlying drivers, we asked:

(i) how crow abundance and (ii) roadkill count vary with land-use, human activity, and country, given that size and complexity of economies can influence agriculture, population distribution, road quality, and consequent travelling speeds. Vehicle speed increases the likelihood of roadkill (see, e.g. Joyce and Mahoney, 2001; Ramp et al., 2006; Gunson et al., 2011; D'Amico et al., 2015), although noise from busy roads can deter wildlife from road vicinities (see e.g. Clevenger et al., 2002). Roads surveyed in this study are not constantly busy, however, so vehicle speed remains a likely predictor of roadkill frequency.

2. Methods

2.1. Study site

We surveyed 1170 km of principal road linking major centres (Kimberly-Cape Town, Pretoria-Bulawayo, Gaborone-Francistown, and Bulawayo-Harare) in SA, Botswana and Zimbabwe in May 2010. As economic size can impact road network size and quality (Banister and Berechman, 2001), we recorded (1) GDP, PPP which represents gross domestic product converted to dollars using purchasing power parity rates (2) GDP per capita, which is the gross domestic product divided by midyear population (World Bank, 2010); Table 1. Speed limits for road transects ranged from 80 to 120 km/h, but actual average speeds were generally lower. We determined average vehicle speed in two ways. We consulted Google Maps, which uses official speed limits, recommended speeds, likely speed according to road type, historical average speed data, and travel times of previous users (Forbes, 2013). Then, travelling at the speed limit, we estimated speeds of vehicles travelling in the same direction as ourselves, using the odometer. Average speeds calculated using the two methods were similar (Table 1). Although GDP per capita is comparable between Botswana and South Africa, South Africa's total GDP is 20 times that of Botswana. Roads are correspondingly busier, and infrastructure is more developed, with cars moving faster on the South African roads we surveyed than those in Botswana and Zimbabwe (Table 1).

Table 1
Economic indices (2010) and average speeds for South Africa, Botswana and Zimbabwe.

Country	GDP, PPP	GDP per capita	Vehicle speed (km/h)	
			Google maps	Odometer
South Africa	$613,916,590,004	$6889	110	114
Botswana	$26,866,632,487	$6882	77	80
Zimbabwe	$19,409,366,289	$995	66	63

2.2. Field methods

Each transect measured 10 km, with at least 5 km between transects. We travelled transects at 70 km·hour^{-1}. The ideal speed for counting roadkill is between 40 and 50 km·hour^{-1} (Guinard et al., 2015), and even at this speed, roadkill on verges can be seriously underestimated (Guinard et al., 2012). However, we assumed that the bias would apply equally across all three countries. For the 5 km stretches between transects, we travelled at the speed limit to help us assess speeds of other vehicles. Transects containing large transmission pylons were excluded, as were towns or cities. SA contained 42, Botswana, 19, and Zimbabwe, 56 transects. Transects were matched for presence of telegraph poles (13–16 km^{-1}), which can be used as perches, and nesting sites (Dean and Milton, 2003). Bird behaviour and likelihood of vehicle-wildlife collision vary with time of day (Visintin et al., 2016). Transects were carried out between 08 h00 and 16 h00 in all three countries. Given that traffic patterns can change over weekends and that this can affect bird behaviour (Bautista et al., 2004), we restricted sampling to weekdays, only. For each transect we recorded date, country, route, pied crow abundance (all individuals within 100 m of the road verge), roadkill count, dominant landuse, and landuse category, a measure of human impact [(a) low density rural: under 10 people, no buildings ("low"), (b) medium density impacts, agricultural or communally grazed: homestead with <20 people per transect ("medium"); (c) evidence of agricultural activities, usually >20 people per transect observed ("high"), but towns avoided], vehicle type (automobile, bus, pickup-truck, lorry), occupants per vehicle, and average vehicle speed (km/h).

Roadkill included vertebrates (reptiles, amphibians, birds and mammals) ranging in size from lizards and frogs to the striped polecat (*Ictonyx stiatus*, maximum weight 1400 g). No large mammal roadkill (e.g. kudu [*Tragelaphus strepsiceros*] domestic cattle [*Bos taurus*] or goats [*Capra aegagrus*]) was observed within transects.

2.3. Data analysis

To assess relationships between crow, and roadkill, abundance and the various explanatory variables, we fitted linear models using generalized least squares. Linear models often allow insights into patterns in the data, whilst correcting for a number of variables (e.g. Valipour, 2015). We set ln (pied crow abundance 10 km^{-1} + 1) as the dependent variable, country, roadkill count 10 km^{-1}, vehicles 10 km^{-1}, mean number of occupants per vehicle, dominant landuse and interactions between these as explanatory variables. For roadkill, we used ln (roadkill count 10 km^{-1} + 1) as the dependent variable and used the same explanatory variables as for crows, save for roadkill. We first tested for spatial autocorrelation using Moran's I. Where such autocorrelation was detected, we also included various spatial correlation structures (i.e., Gaussian, exponential, spherical, rational quadratic and linear, with and without nuggets). All possible combinations of explanatory variables were considered. We selected the most parsimonious model as that with the lowest AIC value (>2 units lower than any others).