Matching theories on kleptoparasitism to a complex avian event in Perth, Western Australia

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Theories on kleptoparasitism are matched to a complex event during which a Laughing Dove *Streptopelia senegalensis* was injured by a car, probably fatally, then depredated by a group of Australian Magpies *Gymnorhina tibicen* and subsequently kleptoparasitized by two Australian Ravens *Corvus coronoides*. Relevant phylogenetic and ecological theories on kleptoparasitism suggest the main factors in play included the ravens' greater size and intelligence (estimated using an encephalization quotient); the prey type being a vertebrate that provides a rich energy source; their prey handling times, which the ravens minimised to their advantage; and the context of an open urban habitat, which facilitated clear observations for the ravens and the magpies.

Keywords: passeriformes, urban, road, terrestrial, corvidae

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INTRODUCTION

Kleptoparasitism is the theft of food already procured by others and can be intraspecific or interspecific (Brockman & Barnard 1979). Kleptoparasites, like predators, are common in both terrestrial and aquatic realms, and amongst vertebrates and invertebrates (Iyengar 2008). However, this paper focuses on terrestrial Aves (birds), with an emphasis on examples from the Passeriformes (Perching Birds) and Corvidae (Songbirds). Kleptoparasitism in birds appears to be a labile evolutionarily trait (Morand-Ferron *et al*. 2007) that is present in some groups more than others; for example, there is a disproportionate number of kleptoparasitic taxa in Laridae (Gulls, Terns), Fregatidae (Frigate birds) Accipitridae (Eagles, Kites and Goshawks) and Corvidae (Brockman & Barnard 1979; Morand-Ferron *et al*. 2007).

Some of the central conditions required for kleptoparasitism include the value of the stolen resource must exceed the costs of the theft, including the cost of the competition (Iyengar 2008). Typical attributes in kleptoparasites are size, greater cognitive ability and aggressiveness (Morand-Ferron *et al*. 2007). In particular, they must have the ability to learn (Brockman & Barnard 1979; Morand-Ferron *et al*. 2007). Species vary in the extent that they adopt kleptoparasitic behaviour. Some use it exclusively (obligate kleptoparasites), whereas others adopt its use optionally or discretionarily (facultative kleptoparasites; Iyengar 2008). Facultative kleptoparasites are usually dietary generalists and opportunists (Barnard 1984; Iyengar 2008). Conversely, hosts typically have a diet including vertebrates, because such prey is energy rich and often requires long handling times (Brockman & Barnard 1979; Morand-Ferron *et al*. 2007).

In addition to the intrinsic requirements of the thieves and hosts, suitable ecological conditions facilitate food theft. Open environments such as two-dimensional grasslands or marine habitats provide greater visibility than closed forests, thus increasing the potential to observe hosts (Morand-Ferron *et al*. 2007). Another factor is the social foraging environment; for example, the multi-species combinations of seabirds (Furness 1987) or heterospecific social foraging groups that share the same foraging habitat (assemblages), which allows group members to observe how conspecifics and heterospecifics forage. In such locales it is obviously beneficial to see the foraging success of others (Brockman & Barnard 1979).

This paper reports a complex, single event incorporating road-injury, predation and klepto-parasitism, and involving three passerine and one non-passerine species. The kleptoparasitism is the main focus of the paper. The event is compared to theories derived from comparative analyses and reviews on kleptoparasitism. Overall, the events observed match theoretical predictions.

METHODS AND RESULTS

Rationale

In order to explain the observed predation and subsequent theft, aspects of each species morphology, behaviour and ecology, along with the urban habitat are related to current theories on kleptoparasitism. An estimate of each species' cognitive ability, i.e. an encephalization quotient (EQ), was calculated from the body mass and brain mass of each species (Table 1). The EQ of each was then assessed to see if it aligned with general theories on kleptoparasitism. Absolute, rather than relative, brain size is considered the best predictor of cognitive capacity (Olkowicz *et al*. 2016). Taxonomy used

Table 1. Encephalization quotient (EQ*) of the four species.

Species	Body mass (gm)	Brain vol. (ml)	EQ
Australian Raven	675	9.83	1.11
Australian Magpie	317	4.65	0.87
Magpie-lark	92	1.68	0.71
Laughing Dove	101	1.24	0.49

*calculated by the ratio of the absolute brain volume to the volume expected for its body size (i.e. bodysize$^{2/3}$):

absolute brain volume / 0.12 × body mass $^{0.66}$ (Jerison 1973).

Species masses are in grams and taken from Dunning (2008).

Brain volume in millilitres from (Iwaniuk & Nelson 2003).

follows Jønson *et al.* (2020). Encephalization is a proxy for intelligence or cognitive ability allowing comparisons between different species with the majority of studies using the encephalization quotient (Mitchell 2016). The encephalization quotient adjusts for disparate taxonomic group using a cephalization factor (0.12 was used in this study; Jerison 1973).

Species backgrounds

The four species involved in the event described below are common to urban settings in Perth, including the locality involved. All four have benefitted in various ways from the changes associated with urbanisation.

The Laughing Dove *Streptopelia senegalensis* is a non-native, granivorous bird, introduced to Western Australia in 1898 (Serventy & Whittell 1976; Johnstone & Storr 1998). Australian Magpies *Gymnorhina tibicen* (hereafter magpies) are well-known opportunists, known to take small birds when the opportunity arises (Fulton 2006), although they are predominately insectivorous feeding mostly on the ground (Floyd & Woodland 1981; Johnstone & Storr 2005). They are highly social birds often seen in groups (Higgins *et al*. 2006), though individuals privately cache food (Rollinson 2002). Australian Ravens *Corvus coronoides* (hereafter ravens) share ground foraging attributes with the magpie, though not entirely. Ravens are broadly omnivorous and generalist carrion feeders; they have benefitted from dead livestock and roadkill (Rowley & Vestjens 1973), as well as scavenging from roads and natural refuges within urban environments (Sazima 2020). Ravens exploit human refuse in densely urbanised areas, showing the capacity to forage more innovatively than other species (Diquelou *et al*. 2016). The Magpie-lark *Grallina cyanoleuca* is granivorous and insectivorous including taking freshwater invertebrates. It feeds predominately on the ground and around water (Johnstone & Storr 1998), and is one of the most successful adapters to urban environments (Kitchen *et al*. 2011).

The observation

In a southern suburb (at 32°20′31.2″S 115°45′44.9″E) of Perth, Western Australia, on 28th April 2014, a Laughing Dove (hereafter dove) was dazed and injured by a passing car. Three Australian Magpies *Gymnorhina tibicen*, from a larger group, attacked the dove as it staggered and fell several times on the road. The magpies pecked the dove's head apparently trying to kill it. Despite the continued pecking it kept struggling and falling, apparently unable to fly. One magpie carried the still alive dove for more than 10 m dropping it on a grassy nature strip and then continued to peck it. A Magpie-lark watching the attack from about 1.5 m away did not attempt to peck the dove, but seemingly waited for an opportunity to do so—the Magpie-lark appeared excited based on its jizz and springy or bouncing movements. Two ravens arrived and watched the dove being carried off the road. At the point when it seemed that no fight was left in the dove, and while the magpies continued to peck, the two ravens approached in stages over approximately 30 seconds. They then flew the final 5 m directly to the disabled dove, stopped and looked briefly at the magpies before taking it from them. The two ravens flew with the dove (one carrying) to a point about 25 m away, then commenced eating it while it was still alive. At this stage I approached for a better view—they may have been aware of me as they then took the dove farther away, although it may be that removing the dove lessened the chances of combat with the magpies. The ravens took the injured dove over a 2.5 m high fence about 5 m from where they had been and continued to pull it apart. The same Magpie-Lark that had approached while the magpies had the dove on the road and again on the grass verge followed the ravens with the dove, whereas the magpies did not. The Magpie-lark did not consume or make contact with any part of the dove, yet it looked as though it wished to join the kill or at least snatch some of the dove.

DISCUSSION

Brain versus brawn

The core of this observation was that two ravens stole a valuable energy-rich resource, which had been the opportunistic prey of the three magpies. This theft might be considered unexpected given that magpies can be aggressive and predatory towards other birds—Fulton (2006) describes magpies killing a Brown Goshawk *Accipiter fasciatus* in brood defence—and are well-known for attacking humans (e.g. Warne *et al*. 2010). The magpies outnumbered the ravens, but individually the mass of a magpie is about 47% of a ravens. Thus, the physical size of the participants suggests that the ravens would be victorious in competition for the dove. However, in a targeted review, Morand-Ferron & Lefebvre (2007) found that the residual brain size was significantly greater in kleptoparasites than their hosts, but body mass was not. Thus, brains and not brawn better explains kleptoparasitism. In the example described the ravens had both a greater body mass and absolute brain volume than the other birds. Consequently their greater brain-to-body ratio, and therefore greater encephalization quotient, suggests a cognitive ability above that of the others. This study found that ravens were more intelligent than the other species, and is supported by a recent urban study measuring innovative foraging, in which ravens outperformed all other measured species by using a greater number of skills that require greater cognitive ability (Diquelou *et al*. 2016).

Although it is counter-intuitive to dismiss that size plays a part, it is accepted that greater cognitive ability increases the probability of success (Morand-Ferron & Lefebvre 2007). In the observed event the raven's greater mass probably helped in securing the dove from the magpies. Fulton (2019) derived a predator-prey mass ratio of 0.25 for nest predators and their prey, using the mean size of adults at prey-nests. In the same study, borrowed data on raptor prey from Olsen *et al*. (2010) indicated a mean predator-prey mass ratio of 0.26. These show that the prey were 75% smaller than the predators. Therefore, it seems likely that greater body mass and cognitive ability both contributed to the ravens taking the dove from the magpies.

Finding and handling prey

Hosts that catch and handle prey are adding value for the thief (Morand-Ferron & Lefebvre 2007; Iyengar 2008). The magpies (the host) invested energy into catching and preparing the dove for consumption, but in doing so added to the prey's value for the thieves (the ravens). The characteristic sequence of predation events is typically: the prey is searched for, acquired and handled, and then consumed after sufficient handing. In that sense, the sequence progressively adds value to the prey. Thus, the thief gains greater benefit from taking the prey later in the handling stage (Hadjichrysanthou *et al*. 2018). This is exactly how the ravens behaved in the event described, i.e. they maximised their benefit (and minimized their efforts) by delaying the theft.

Vertebrate prey and phylogeny

Large prey that require greater handling times are favoured by and are more profitable to kleptoparasites (Iyengar 2008). Host species are usually characterised as frequently preying on vertebrates (Morand-Ferron & Lefebvre 2007). By comparison, kleptoparasites are commonly considered predatory and dietary opportunists (Brockmann & Barnard 1979). Predators familiar with finding and handling vertebrate prey are thought to be pre-adapted to kleptoparasitism (Brockmann & Barnard 1979). Brockmann & Barnard (1979) further highlighted that almost all kleptoparasitic bird families were predators that included vertebrate prey in their diet. They indicate that the Accipitridae, Laridae in the non-Passeriformes and Corvidae in Passeriformes have significantly more kleptoparasites than other families. In Australia, there are few reports of kleptoparasitism in Passeriformes, although the few that have been published are concentrated within the Corvidae and Artamidae, and the thieves were considered more facultative than obligate (Lepschi 1990; Robinson 1993; Fulton 2005; Recher & Davis 2005). Furthermore, Krohn (2016) highlighted *Corvus* species as kleptoparasites including the Australian Raven. Many members of this family (Corvidae) are kleptoparasites due to their cognitive superiority to most other birds (Emery 2006). In addition, they have forebrain neuron counts equal to or greater than primates with much larger brains (Olkowicz *et al*. 2016).

Conspicuousness of vertebrate prey

As discussed above vertebrate prey are associated with kleptoparasitism by providing more energy and by being conspicuous. They are large, mobile and take longer to handle, which makes them conspicuous to kleptoparasites (Morand-Ferron & Lefebvre 2007). With three magpies undertaking the handling of the dove, they were conspicuous enough to attract the ravens, the Magpie-lark and myself. The stumbling of the dove, after being hit by a car, was undoubtedly the initial stimulus presenting a conspicuous image on a featureless surface—the road. The presence of car and magpies is commonplace; without the image of the injured dove such things would pass without being noticed.

CONCLUSION

A group of factors interacted in this short event. The open environment of the road facilitated kleptoparasitism, by making its events conspicuous. The prey was a rich energy source making it valuable enough to steal. Ravens and magpies share the same social habitat within the same assemblage. The ravens were the largest and most intelligent bird in this group, their greater intelligence fitting the contemporary theory that kleptoparasites are more intelligent than their hosts. I suspect that urban birds will continue to be killed or injured in this manner, so such events must be more commonplace than has been reported.

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