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The Scavenging Behaviour of the Australian Raven (Corvus Coronoides): Patterns and Influencing Factors

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Comments

The scavenging behaviour of the Australian Raven (*Corvus coronoides*): patterns and influencing factors

Nekrofagické chování krkavce australského (Corvus coronoides): *průběh a ovlivňující faktory*

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The Australian Raven (*Corvus coronoides*) is a widespread, abundant corvid which is often considered a pest species, due to the thought that it predates on livestock, ruin crops, and is often seen feeding on refuse, in both urban and rural areas. The species is known to feed on a range of material from seeds in ploughed fields to human refuse and decomposing organic material. A large proportion of its diet consists of carrion, and as such, the Australian Raven is an effective detrivorous species capable of removing and consuming dead and decomposing carcasses. This research examined the scavenging pattern of the Australian Raven on domestic pig (*Sus scrofa*) carcasses at four different locations surrounding Perth, Western Australia. Domestic pig carcasses were sacrificed and placed in outdoor environments and the carcasses were filmed using infrared cameras with time-lapse image capture. The number of feeding events, length of feeding, material being fed upon, and associated weather data were recorded. Furthermore, the influences of location, season and life cycle of the Australian Raven on scavenging behaviour is examined. It was found that raven scavenging intensity was greatest during spring and as an omnivore there was significantly higher feeding on both flesh and insects in one event than either material on its own.

Krkavec australský (Corvus coronoides) *je široce rozšířeným a početným druhem, který je často považován za škodlivý druh v souvislosti s domněnkou, že preduje na hospodářských zvířatech, ničí zemědělské plodiny a je znám jako druh živící se odpadky. Z dosavadních poznatků víme, že má široké potravní spektrum sahající od rostlinných semen přes odpadky až po rozkládající se organický materiál. Mršiny tvoří značnou část jeho potravního spektra, čímž se řadí mezi velice efektivní detrivorní druh, likvidující mrtvoly zvířat a rozkládající se mršiny. V naší práci jsme zkoumali nekrofagické chování tohoto druhu na zdechlinách domácích prasat na čtyřech lokalitách v okolí Perthu v Západní Austrálii. Mršiny prasat byly umístěny ve volné přírodě a průběh krmení se ptáků na nich byl natáčen pomocí pomaloběžných videokamer. Po celou dobu výzkumu jsme zaznamenávali počet krmících se událostí, jejích délku, typ požíraného rozkládajícího se materiálu a počasí. V práci rozebíráme význam jednotlivých* *lokalit, vliv roční doby a životního cyklu krkavců na požírání mršin. Zjistili jsme, že intenzita požírání mršin byla největší na jaře. Z hlediska druhu jako omnivora bylo intenzivnější současné požírání jak mršin tak i hmyzích larev z těchto mršin během jednoho krmení než při požírání jen jedné z těchto potravních složek samostatně.*

Keywords: decomposition, detrivorous species, necrophagy, taphonomy, Western Australia

INTRODUCTION

Scavengers play a significant role in the ecological stability of the environment (DeVault et al. 2003). The scavenging activity can be observed on natural kills (Wilmers et al. 2003) or with human interference as with 'vulture restaurants' (García-Ripollés et al. 2004) or feeding stations (Skagen et al. 1991). This pulse of nutrient resources will not only assist obligate scavengers such as vultures and condors (Ruxton & Houston 2004) but create facilitative scavengers (Brooker & Ridpath 1980, Stahler et al. 2002). These facilitative scavengers not only exploit the pulse of nutrients but can predate on surrounding animals (Cortés-Avizanda et al. 2009). This research looks at the response of the Australian Raven to the appearance of a pig carcass as a source of readily available nutrients.

In Australia, there are five abundant corvid species including the Australian Raven (*Corvus coronoides*), Little Crow (*Corvus bennetti*), Torresian Crow (*Corvus orru*), Forest Raven (*Corvus tasmanicus*), and Little Raven (*Corvus mellori*) (Rowley 1973b). The crows, *C. orru* and *C. bennetti*, are distributed in the tropical and arid regions of the continent while the ravens are found in the temperate, southern regions. In southern Western Australia, and specifically around Perth, only *C. coronoides* and *C. bennetti* are present, with *C. coronoides* being much more abundant. *C. coronoides* is often associated with human habitation and is known to feed on human refuse and decomposing organic material (Rowley & Vestjens 1973).

Australian Raven is often considered a nuisance or pest species and has been classified as such by the West Australian Department of Agriculture's *Agriculture and Related Resources Protection Act 1976* which allows for the species to be controlled under a management scheme. This, however, does not consider the fact that the raven is an effective detrivorous species that performs an essential ecological role by consuming dead and decomposing organic material. This material ranges from refuse located in rubbish bins and strewn about urban areas to dead animals killed on the roads in suburban and rural areas. Flesh accounts for up to 60% of the birds' diet during winter and spring, however they are inefficient predators and therefore their major source of flesh is through scavenging. Occasionally, predation by *C. coronoides* has been observed on larger animals such as lambs, however these attacks are generally on sick or dying animals (Rowley et al. 1973). Those birds that were seen scavenging were also noted to have eaten not only the flesh of the carcass but also the insect material associated with the decomposing carcass (Rowley et al. 1973).

Food

Australian Raven is a true omnivore, having an extensive range of items which it will consume. From examination of stomach contents it is evident that the proportion of different materials eaten depends on the location of feeding and the season. Rowley and Vestjens (1973) have reported stomach contents of 34% flesh, 42% invertebrates, and 24% plant material from birds in New South Wales. The main sources of flesh in rural areas include carrion, crustaceans (yabbies *Cherax* spp.), and lambs that are scavenged from natural deaths. Sources of plant material include grains from planted fields and seed waiting to be ploughed into the ground for the next season's crops. Invertebrate sources include both adult and immature insects (maggots and/or pupae). The adult invertebrates which can be consumed include beetles, grasshoppers, and spiders (Rowley et al. 1973). The variation in feeding by location has been demonstrated by a comparison of birds which live in an urban environment and those that live in a rural area. Examination of the stomach contents of birds in the urban environment has demonstrated that they feed on carrion noted by maggots as well as other items associated with feeding in rubbish bins including glass, plastic, rubber, metal, and other non-food items. While the stomach contents of rural birds did show carrion ingestions they lacked the non-food items and had more insects and grain material (Rowley et al. 1973).

Breeding

The breeding season begins in July, peaks in August and declines in September, occasionally lasting into October (Rowley et al. 1973, Schodde & Tideman 1986). The female lays one to six eggs, with a mean clutch size of 4.44 (Rowley 1973a). The incubation period is approximately twenty days. The female incubates the eggs while the male patrols the territory (Schodde et al. 1986). Upon hatching, the young stay in the nest until fledged at approximately 43 days. The parents continue to feed the young for several months after they have left the nest but by three months the young are foraging for themselves (Rowley 1973a).This study was designed to determine the scavenging patterns of the Australian Raven at four locations around Perth, Western Australia. Furthermore, the influences on these patterns, such as season, weather and the presence/absence of competing species, were examined. Pig carcasses were used as attractants for the birds and all activity was videoed and recorded for all relevant information. The data collected were examined for any relationships as well as differences that can be observed.

MATERIAL AND METHODS

Eighteen domestic pig carcasses (*Sus scrofa*) weighing between 40 and 50 kg were used in this study to investigate scavenging rates on animal carcasses. The pigs were killed using approved sacrifice methods and sanctioned by the ethics committee at the University of Western Australia (Approval number RA/3/100/351). The pigs were placed on the ground at the experimental sites with no artificial covering.

Images were collected using infrared (IR) cameras, either a Sanyo (model VC9212B/WCCD) or a Panasonic CCTV infrared camera (model WV-BP334EE) with a Microlight infrared illuminator (IR -21/25-880). Two cameras were used at different locations when two replicates were running simultaneously. These cameras filmed in black and white both during the day and night under IR conditions. Images were initially captured with a Sanyo TLS-1600P time-lapse video cassette recorder which allowed for three days of recording before the tape was changed. Later images were captured with a D-TEG SRX1004 4-chanel digital video recorder which allowed for several months of image capture before being downloaded. Both instruments were set to record at two frames per second. This allowed for a large amount of data to be recorded yet the frame rate was sufficient to capture the presence of any animals which would be feeding on the carcasses.

Data collection

The captured images were viewed and data collected in relation to the location of the experiment, the season, the type of location, the carcass replicate number, and the experimental day. Pig carcasses were placed on experimental day zero and subsequent days were counted from midnight to midnight. Experimental days were recorded in their entirety whether or not any feeding events occurred during the day or night. When feeding was observed on the video imagery, the species of animal and the start and end time of the event were recorded. From these times the duration of each event was calculated. A feeding event was classified as a single event if less than ten minutes elapsed from the time the same animal had left and returned to the carcass. If ten or more minutes of an absence of feeding occurred then the events were deemed to be unique and recorded separately. Once the number of feeding events on each carcass was observed the intensity of scavenging was calculated. That was the average number of feeding events each day by individual carcasses. During each feeding event any movement of the carcass was noted. We also recorded whether the animal fed directly on the carcass or on the associated insect material. This was determined by the location of feeding (i.e. around the carcass or at the orifices) and the effects on the carcass (removal of flesh).

The pig carcasses were placed out during all seasons of the year. The replicates were allowed to continue until the carcass had reached the skeletonization stage of decomposition. This stage was identified by the carcasses having the majority of the skeleton exposed and the only soft tissue remaining was either mummified or strictly cartilage. The only modification to this procedure occurred when the carcass was removed by scavenging activity, only seen at Shenton Park from the activities of the Red Fox (*Vulpes vulpes*).

A data logger was placed at each experimental site to record the temperature during each replicate. The rainfall measurements were obtained from the nearest Australian Government Bureau of Meteorology weather station.

Experimental locations

Four distinct locations were used for the experiments, all of which were unique in their floral and faunal composition and were within 250 km of Perth, Western Australia. The first location utilised a fenced native reserve located 20 km south of the Perth central business district (CBD) in the suburb of Jandakot (32°09'S 115°49'E). The reserve is surrounded by a fox-proof fence that is maintained by the caretaker and all non-native animals are removed and excluded from the location, except Rats (*Rattus rattus*) and European Rabbits (*Oryctolagus cuniculus)*. Within the reserve there are many native mammals and reptiles including Western Grey Kangaroo (*Macropus fuliginosus*), Black-gloved Wallaby (*Macropus irma*), Quenda (*Isoodon obesulus fusciventer*), Brushtail Possum (*Trichosurus vulpecula hypoleucus)*, Rosenberg's Heath Monitor (*Varanus rosenbergi*), Bungarra (*Varanus gouldii*) and Bobtail Skink (*Tiliqua rugosa*). The avian species which frequent the reserve include Australian Raven, Willie Wagtail (*Rhipidura leucophrys*), Brown Honeyeater (*Lich-*

mera indistincta), and others not associated with feeding on or around the carcass. Experimental placement of the carcasses within the reserve was on the edges of a Paperbark (*Melaleuca* spp.*)* swamp in a moderately wooded area. Dominant vegetation at the site included Jarrah (*Eucalyptus marginata*), Marri (*Corymbia callophylla*), Paperbark, Grass tree (*Xanthorrhoea* spp.), and Banksia (*Banksia* spp.). The understorey was lightly vegetated without any areas of heavy grass growth.

The second location utilised a suburban site located five kilometres from the Perth CBD at a research facility owned by the University of Western Australia in the suburb of Shenton Park (31°57'S 115°47'E). The facility is fenced against human intrusion but the barrier is easily crossed by animals. The facility is frequented by Red Fox, Australian raven, Kookaburra (*Dacelo novaeguineae*), Willie Wagtails, and several other species that were seen infrequently. The land is mixed use with native bushland including Jarrah and Sheoak (*Casuarina* spp.), sheep paddocks, netted fields for growing commercial crops, crustacean rearing ponds, and grape vines.

The third location was located at Perup Nature Reserve (34°11'S 116°35'E) which is approximately 300 km south east of the Perth CBD. The reserve is protected under the Western Shield program run by the Western Australian government which is designed to remove feral animals from the native bush and reintroduce those native animals which were endangered by the feral animals (Department of Environment and Conservation 2007). Species found within the reserve include Western Grey Kangaroo, Black-gloved Wallaby, Tammar Wallaby (*Macropus eugenii*), Quokka (*Setonix brachyurus*), and Woylie (*Bettongia penicillata*). Native carnivores were found only at this location and included Chuditch (*Dasyurus geoffroii*), Brush-tailed Phascogale (*Phascogale tapoatafa*), Mardo (*Antechinus flavipes*), Grey-bellied Dunnart (*Sminthopsis griseoventer*) and the insectivorous Numbat (*Myrmecobius fasciatus*). Native and feral rats have also been observed within the reserve including the Water Rat (*Hydromys chrysogaster*) and Bush Rat (*Rattus fuscipes*). The avian species present include Australian Raven, Wedge-tailed Eagle (*Aquila audax*), and many seed and insect eaters. The flora in the experimental area was dominated by Jarrah, Marri, and Sheoak trees. The understorey contained Grass trees, a few Zamia palms, and several low *Dryandra* bushes.

The fourth location was Watheroo National Park (30°11'S 115°44'E) which is 200 km north of the Perth CDB. Only avian species were observed at this location and included Australian Raven, Hooded Plover (*Charadrius rubricollis*), and Willie Wagtail. The area is also frequented by Wild Boars and Red Foxes. The area of experimentation contains limited numbers of large trees, mainly banksias, with many *Dryandra* spp. and *Melaleuca* spp. scrub bushes in the area.

Statistical analysis

Statistical analysis was conducted using Genstat© 9th edition and SPSS® 13th edition. Initially frequency tables were calculated to determine trends in the data which needed to be examined by further testing. Linear regression was used to determine relationships between variables of weather, scavenging, and decomposition. Discriminant and principal component analyses were conducted to differentiate locations and seasons. ANOVA determined differences between factors of several aspects of the research.

RESULTS

Scavenging patterns

Australian Raven was the most prolific omnivore observed, indeed the most prolific scavenger, at all experimental sites except Perup (where Bungarra was the most common) (Table 1). It was an almost exclusively diurnal feeder, eating both the flesh of the carcasses and associated insects. The intensity of scavenging by the birds at Jandakot was significantly higher than at Perup or Shenton Park ($F_{3,66}$ = 7.25, p < 0.001) and the cumulative time ravens spent scavenging at Jandakot was significantly greater than at any other location ($F_{3,66}$ = 8.76, p < 0.001). Once allowance was made for the unequal representation of carcass placement by season (by using location as a blocking factor) in the different locations, spring emerged as the dominant scavenging season for the Australian Raven, with significantly more incidents of scavenging than in summer or autumn ($F_{3,63}$ = 2.82, p = 0.046).

There was marked variation between locations in the diurnal scavenging pattern of ravens (Fig. 1). At Shenton Park they scavenged continuously throughout the day, while at Perup activity was highest in the morning and decreased during the course of the day. Only at Jandakot and Watheroo were there pronounced morning and afternoon periods of intense raven feeding. At Watheroo in particular there was very little raven activity around noon.

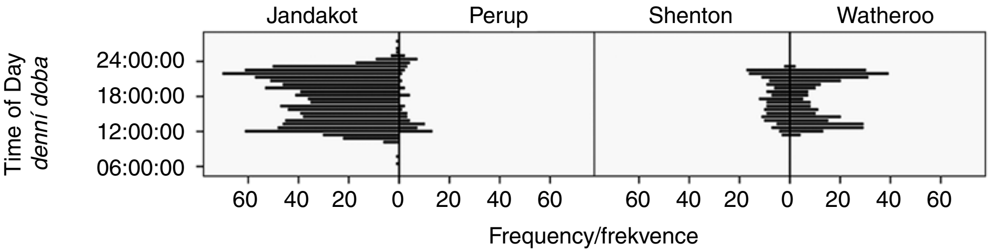

Fig. 1. Australian Raven (*Corvus coronoides*) feeding times by location for all locations and decompositional stages.
Obr. 1. *Doba krmení se krkavce australského* (Corvus coronoides) *rozdělená dle umístění pro všechny lokality a stupně rozkladu mršin.*

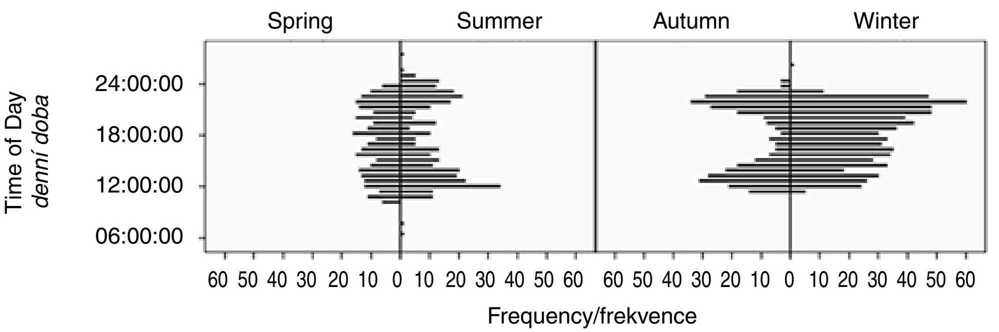

Fig. 2. Raven feeding times by season for all seasons and decompositional stages.
Obr. 2. *Průběh krmení se krkavce australského na mršinách prasat. Průběh je rozdělen do čtyř ročních období a stupňů rozkladu.*

Table 1. Animals observed scavenging at all locations.
Tab. 1. *Seznam druhů, které byly pozorovány při požírání mršin prasat na všech čtyřech lokalitách.*

location *lokalita*	species *druh*	number of feeding events *počet krmení*	day of first appearance *den prvního výskytu*	mean temperature at each feeding (°C) *průměrná teplota při krmení (°C)*	mean length of each feeding (sec.) *průměrná délka (v sek.) krmení*
Jandakot	Australian Hobby	1	20	17.80	60
	Australian Raven	999	0	17.28	1707
	Bat	31	2	17.44	139
	Bobtail	47	2	21.80	370
	Brown Honeyeater	501	0	17.16	964
	Brushtail Possum	415	10	17.33	1968
	Bungarra	22	1	24.07	401
	Echidna	1	2	17.30	60
	Frog	24	0	17.07	1527
	Mouse	5	2	14.58	672
	Quenda	286	0	16.22	1260
	Rat	226	0	17.79	1598
	Wedgetail Eagle	11	1	15.69	4456
	Western Blue Tongue Skink	1	24	24.25	60
	Western Grey Kangaroo	5	1	15.55	132
	Willie Wagtail	298	2	16.69	857
Perup	Australian Magpie	1	17	24.90	780
	Australian Raven	69	2	22.05	985
	Bobtail	10	4	22.75	948
	Brushtail Possum	19	1	23.26	433
	Bungarra	98	1	23.20	1152
	Chuditch	90	0	22.30	626
	Crevice Skink	2	4	20.00	330
	Dunnart	4	0	23.11	75
	Hooded Robin	91	0	19.07	533
	Red Fox	2	18	29.73	510
	Ringtail Possum	4	6	20.78	165
	Wedgetail Eagle	1	1	17.00	300
Shenton	Australian Magpie	1	7	27.70	60
	Australian Raven	174	0	14.61	397
	Bobtail	2	2	20.48	210
	Dugite	2	3	22.60	540
	Galah	3	12	14.27	80
	Kookaburra	7	7	25.26	531
	Little Corella	2	17	13.35	210
	Red Fox	82	4	18.36	656
	Western Ringneck	1	5	14.95	240
	Willie Wagtail	23	1	22.31	420
Watheroo	Australian Raven	310	1	16.63	400
	Hooded Plover	26	4	12.04	346
	Willie Wagtail	77	2	12.23	241

There were also marked variations in the diurnal pattern of raven scavenging across seasons (Fig. 2). While scavenging was evenly spread through the day in the warmer seasons of spring and summer, in winter the intensity of scavenging climbed during the day to a peak in the late afternoon. In autumn there were pronounced peaks of raven activity in the morning and late afternoon.

There was a significantly higher amount of feeding by ravens on a combination of insects and flesh (mean ± SE: 81.87 ± 1.13 events per replicate) than on either flesh (13.57 ± 1.65 events per replicate) or insects (13.47 ± 1.06 events per replicate) individually ($F_{2,36}$ = 11.30, $p < 0.001$). This difference was seen across the year and seasonality of feeding was not significant.

Influences on the Australian Raven scavenging rates

Ravens were observed feeding at all locations and during every season, however they were almost exclusively observed feeding during the daylight hours. At Perup more feeding events were observed around dawn than during the day or at dusk (Fig. 3, unbalanced ANOVA, time of day: $F_{3,261}$ = 13.02, $p < 0.001$, location: $F_{3,261}$ = 11.13, $p < 0.001$, interaction: $F_{9,261}$ = 1.47, p = 0.161, decompositional stage effects as blocks). The highest overall intensity of scavenging by ravens was observed at Jandakot. Furthermore, at the other sites

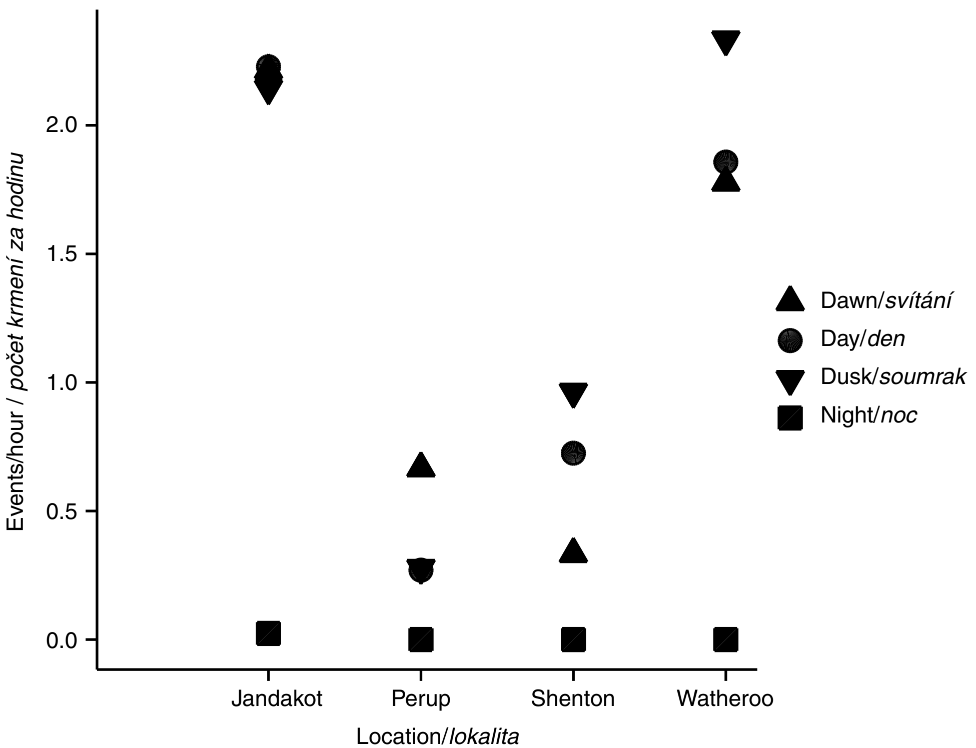

Fig. 3. Mean number of raven feeding events/hour by time of day and location.
Obr. 3. *Průměrný počet krmení za hodinu u krkavce australského. Data jsou rozdělená podle lokalit a částí dne.*

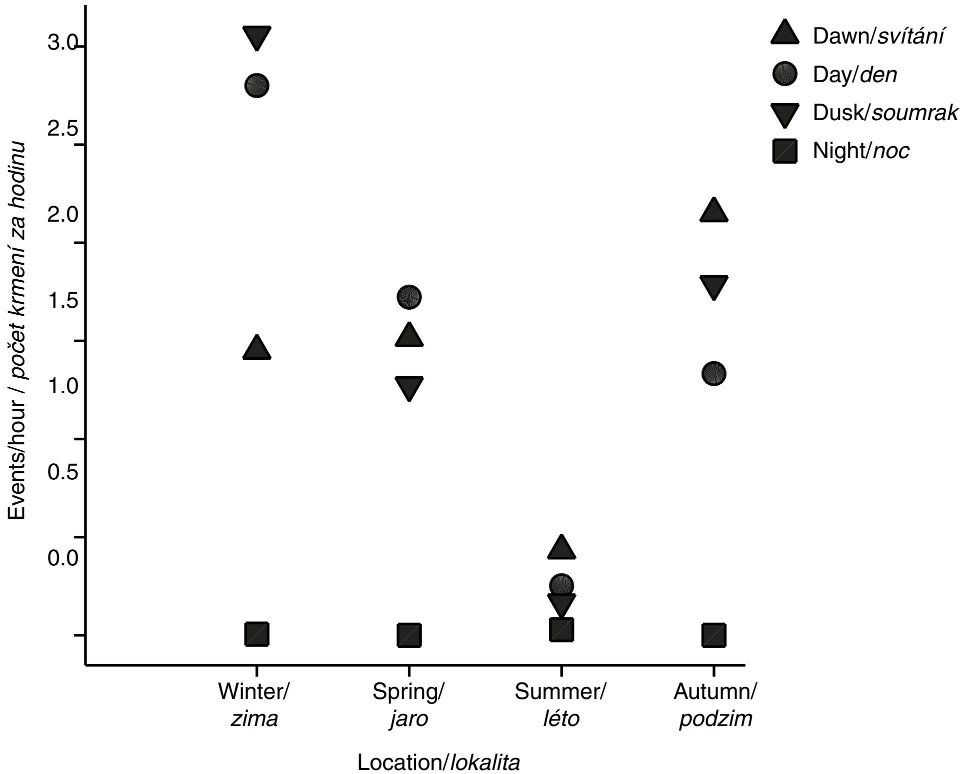

Fig. 4. Mean number of raven feeding events/hour by time of day and season.
Obr. 4. *Průměrný počet krmení za hodinu u krkavce australského. Data jsou rozdělená podle roční doby a částí dne.*

where predators (both native and feral) were observed, raven scavenging was at a lower intensity.

In all seasons except summer the intensity of raven feeding events around noon were less than at all other times of the day. In winter the intensity of scavenging at dusk was greater than at dawn or during the daytime (Fig. 4, unbalanced ANOVA, time of day: $F_{3,261}$ = 13.51, $p < 0.001$, season: $F_{3,261}$ = 11.01, $p < 0.001$, interaction: $F_{9,261}$ = 2.78, p = 0.004, decompositional stage effects as blocks).

There was no relationship between the length of individual feeding events and mean daily temperature or rainfall (temperature: R^2 = 0.00, t_{1550} = 0.63, p = 0.529, rainfall: R^2 = 0.00, t_{1550} = –0.46, p = 0.647). There was a significant negative relationship between mean daily temperature and the daily intensity of raven scavenging ($F_{7,62}$ = 2.13, p = 0.044). That is, when the temperature increases the number of *C. coronoides* scavenging events decreases. Further, there was a trend towards significance with respect to mean daily rainfall and daily intensity of raven scavenging ($F_{1,68}$ = 2.14, p = 0.053), with feeding intensity being less when rainfall was higher. Spring had significantly higher levels of *C. coronoides* scavenging than seen in any other season, however mean daily temperature and rainfall during spring were similar to those in autumn, indicating other influences upon raven scavenging.

There was a strong relationship between the level of scavenging by the birds and their reproductive cycle. There was more scavenging by ravens during the time when they had young or juvenile birds to feed than at any other time (Fig. 5a, unbalanced ANOVA, $F_{3,66} = 2.95$, $p = 0.037$), whether or not variations in activity between locations were taken into account (Fig. 5b, unbalanced ANOVA $F_{3,62} = 2.04$, $p = 0.118$).

The presence of other carnivorous species appeared to influence the amount of time ravens spent scavenging on carcasses (mean ± SE time scavenging with carnivores present 564 ± 2006, and lacking carnivores 1397 ± 4739), however this difference was not statistically significant ($F_{1,68} = 0.43$, $p = 0.445$). There was however, less daily scavenging events in locations where carnivores were present with ~3 fewer scavenging events per day ($F_{1,68} = 12.33$, $p < 0.001$).

DISCUSSION

Australian Raven scavenging pattern

The abundance of the Australian Raven is apparent as it is seen in almost every environment surrounding Perth, Western Australia. The significantly higher number of ravens as well as scavenging intensity at Jandakot can be explained by the fact that this particular site is protected from land-based predators by a surrounding fence. The reserve provides a safe place to roost at night and is small enough to allow the raven

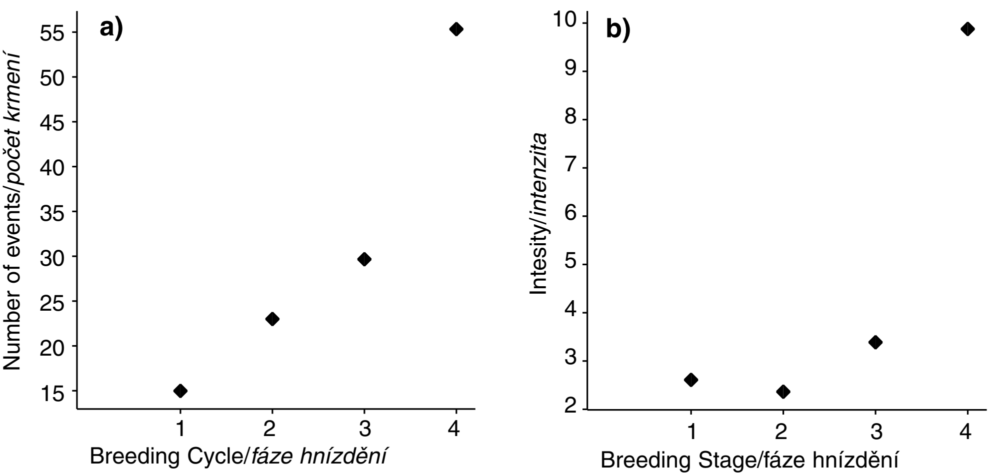

Fig. 5. Mean daily intensity of raven scavenging by phase of the breeding cycle a) Mean number of raven scavenging events by time in the breeding cycle for all locations, b) Mean intensity (defined as the average number of feeding events each day by individual carcasses) of raven scavenging by stages of breeding with location effects eliminated. Breeding cycle: 1 – outside of the breeding season, 2 – onset of breeding until egg laying, 3 – from egg laying until hatching, 4 – from hatching until juvenile independence.

Obr. 5. *Průměrná denní intenzita krmení se na mršinách dle fází hnízdního cyklu* ***a)*** *průměrný počet krmení se za všechny čtyři lokality dohromady,* ***b)*** *průměrná intenzita krmení se (definovaná jako průměrný počet krmení za den na jednotlivých mršinách) po odstranění vlivu lokality. Fáze hnízdění: 1 – mimo hnízdění, 2 – počátek hnízdění až po začátek snůšky, 3 – od snůšky až po líhnutí mláďat, 4 – od vylíhnutí až po osamostatnění mláďat.*

to leave during the day to forage in surrounding areas. Forensically based experiments are conducted on a regular basis within the reserve, all using pig carcasses as human analogues. Although these carcasses are generally protected from scavenging activities by wire coverings, once the experiments have concluded the protection is removed allowing the ravens to scavenge freely. Due to the experiments conducted at the site, the birds are likely to have associated decomposing pig carcasses as an easy source of protein. The frequency of decomposition experiments at the reserve provides the local ravens with a food source not available to ravens at the other study sites. This may have anthropogenically inflated the population size of the raven at Jandakot, accounting for the greater number of observations of scavenging birds.

This influx of ravens for facilitative scavenging could also have the effect of endangering other animal species in the area. The introduction of 'vulture restaurants' to feed obligate scavengers have been shown to increase the number of facilitative scavengers in that given area (García-Ripollés et al. 2004). The increase in facilitative scavengers can also increase predation of animals in the local ecosystem (Cortés-Avizanda et al. 2009). Although the experimental location of Jandakot was not created as a so called 'vulture restaurant' with the placement of pig carcasses could have created greater predation threats on the native animal populations.

Western Australia lacks true specialist scavenger avian species such as vultures and condors. True scavenging avian species are large-bodied and require large amounts of food to cope with the energy demands of searching for food. There is not a sufficient density of large native animals in Australia to have supported the co-evolution of large-bodied detritivorous avian species. Since large domestic livestock were not introduced to Australia until the last 200 years, no large avian predators or scavengers have evolved with them, leaving the niche to be filled by birds such as the Australian Raven and Wedge-tailed Eagle (Ruxton et al. 2004), both of which were observed in our study. The relative infrequency of observations of the Wedge-tailed Eagle compared with the Australian Raven reflects its position as the apex raptor throughout Australia. Apex species tend not to be prolific and are seldom seen in areas of high human population densities (Ridpath & Brooker 1987). A study of the scavenging of ungulate carcasses by White-tailed Eagles (*Haliaeetus albicilla*) showed that this apex raptor was seen at fewer carcasses (27.1%) and engaged in fewer feeding events than other avian species (Selva et al. 2005).

Australian Raven was the principal flesh feeders at most sites except at Perup where the Chuditch was the primary flesh eater. Their behaviour resembled that of Turkey Vultures (*Catharses aura)* in their tendency to feed at the carcasses in groups (Morton & Lord 2006). In most cases no more than four to five birds were present at the body at any one time (exact counts are difficult as birds often flew in and out of camera view) but on at least one occasion a flock of 12 birds, as many as could fit around the carcass, fed together. This concentration of ravens around the carcass was accompanied by intense fighting between birds.

In our study, ravens were seen at carcasses within minutes of their deposition at the Jandakot site (Table 1). In an ecological study in Yellowstone National Park, Wyoming, Stahler et al. (2002) found that it took less than five minutes for ravens to discover a wolf-killed carcass, (having followed the grey wolves as they hunted), and just over 35 minutes to find a carcass which had been deposited by researchers. They also found the number of ravens around a wolf-killed carcass to be significantly greater than around a non wolf-killed carcass. Since there are no natural predators of mammals as large as pigs or humans in Western Australia, it is unlikely that behavioural adaptations to hunting are likely to be a feature of the local raven populations. Their adaptation to rapid orientation to any material deposited by humans can be attested to by any of the local councils or institutions which have been forced to invest in raven-proofing litter bins (Staff Writer 2007). Skagen et al. (1991) found the American Crow (*Corvus brachyrhynchos*) to be relatively unaffected by the presence of humans, allowing them to approach to within 100 m before abandoning a carcass they were scavenging. Thus, crows gained more scavenging time at carcasses than raptors. Furthermore, disturbance did not affect the amount of food consumed from a carcass by crows. In Western Australia ravens scavenging road kill allow both cars and people to approach to within improbably short distances before taking flight. This behaviour, like that of the crow, allows the raven to scavenge on carcasses that would be left undisturbed by other scavenging guilds or at the least allowing them to feed longer and obtain more protein than other animals.

Influences on the scavenging patterns of the Australian Raven

High temperatures can limit scavenging in a number of ways, the most obvious through direct challenge to thermoregulation. Schleucher (1993) summarises the limited physiological thermoregulatory capacities of desert-dwelling birds and their dependence upon behavioural mechanisms such as sheltering and inactivity during the hottest periods of the day. The second major challenge posed by high temperatures, of particular relevance in the Western Australian context, is the water cost of thermoregulation. Whether behavioural (panting, licking) (Dawson & Bennett 1978, Larcombe 2002) or metabolic (Dawson & Wolfers 1978) responses to thermal load incur water loss in an environment where dehydration is a major threat (Porter et al. 2000). While scavenging from carcasses may itself provide a significant source of water in a dry environment, small bodied animals with high energy and water requirements cannot afford to travel far before exhaustion and water loss become limiting factors to their scavenging capacity (Dawson & Wolfers 1978). Thus, the dominant adaptation to heat load amongst Western Australian birds, as well as mammals, is shelter and inactivity above threshold ambient temperatures (Dawson & Wolfers 1978, Brigham et al. 2000, Geiser & Pavey 2007). This was noted in our study in the reduction in scavenging frequency by ravens during the day in the hotter months.

Temperature can also affect scavenging by the effects it has on carcasses. Heinrich (1988) comments upon the way freezing of carcasses limited the capacity of some species to feed upon them in Maine, USA. Conversely, in Australia, extreme heat can accelerate desiccation and mummification of carcasses (Mann et al. 1990). If skin mummifies before it has been ruptured, it can create a hard shell over the decomposing organs and muscles, barring access to any but the strongest and most carnivorously adapted species.

No significant effect of precipitation

on the level of scavenging was observed in this West Australian study, but it would have been difficult to establish such an effect given the infrequency with which rain occurred. While rain fell on 158 days of the 450 experimental days, on 41 of those occasions only trace amounts (<0.5 mm) were recorded. Few scavenging events were recorded on the rare days of extreme rainfall (> 30 mm). Determination of the extent to which 'normal' scavenging patterns were disrupted by the drought conditions experienced throughout much of our study would require replication of the study during periods of average rainfall – certainly not possible within the scope of the study. With the possibility of permanent climate change it may well be in any case that the conditions observed over the duration of this study will be 'typical' and of greatest relevance for the foreseeable future (White et al. 2004).

As mentioned previously, Western Australia was experiencing a drought during the period of this study and animals ran the risk of dehydration in the effort to obtain food. Both birds and mammals expend water when travelling (Goldstein & Bradshaw 1998, Giladi & Pinshow 1999, Porter et al. 2000), especially in the heat of the day. If moisture cannot be obtained from the food itself, then a source of fresh water must lie within a short travelling distance. Maintenance of a water balance is particularly difficult when the animal is of small size (Nagy et al. 1991). The lack of visits by land mammals to the carcasses deposited at Watheroo may have been accounted for by the absence of permanent water holes or water troughs for livestock in the near vicinity. While the carcass itself provides a brief source of fluids, smaller animals would still find it difficult to reach them before dehydrating.

The way in which the energy budget is balanced varies across the reproductive cycle, with the point of greatest energy demand varying with the species (Ryan 1976, Adriano & Calver 1995, Wayne et al. 2005). Animals will time breeding cycles in different ways in order to most effectively utilize the available energy resources. Additional energy demands associated with breeding can include those associated with building a nest (Weathers & Seymour 1998), laying eggs, internal nourishing and birthing of live young (Bonnet et al. 1998), and raising the young in the case of birds and mammals. Alternative strategies to cope with these demands include an early increase in feeding to build up reserves, then decreased expenditure of energy in hunting or foraging and gradual depletion of that reserve during pregnancy and the care of newborn young (e.g. bears) or intensification of food-procuring activities at the time of greatest demand (e.g. birds) (Bonnet et al. 1998).

In this study the raven had a higher scavenging intensity when there were juvenile birds in the nest than at any other time of year, and a relatively low intensity in the period immediately following. This is as to be expected, as the adults have not only themselves but their young to feed. As both parents are food providers to the young (Rowley 1973a), there is pressure for the parents to take only short periods to feed before returning to the nest to allow the other parent to leave and feed. None of the other reports of scavenging by corvids (Heinrich 1988, Skagen et al. 1991, Travaini et al. 1998, Stahler et al. 2002, Selva et al. 2005) address the issue of the influence on scavenging of variation in energy demands in relation to the breeding cycle. The lack of data on other avian species for all phases of the breeding cycle in our study prevented effective analysis of the relationship of reproductive activity to scavenging.

Further research needs to be conducted in more locations to gain a better understanding of the complete ecosystem. Also a project where the birds are caught and banded so that individual birds can be tracked would be invaluable.

Conclusions

The Australian Raven was the most abundant avian scavenger in most experimental locations conducted in this research. The birds were diurnal scavengers with a higher frequency of scavenging in autumn and winter. Although this species was not responsible for the greatest amount of tissue loss from the carcasses in singular feeding events it is likely to have removed the most amount of tissue in total from all carcasses. Small skeletal elements were dispersed by direct action of the ravens; however larger elements were only shifted and not moved great distance. This makes the raven an effective remover of decomposing organic material which otherwise would be a problem that needs to be addressed by public works.

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