



# Social scavenging by wintering striated caracaras (*Phalcoboenus australis*) in the Falkland Islands

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## Abstract

Avian scavengers perform vital ecosystem services by removing waste and slowing disease, yet few details are known about the process of carcass depletion, or the role of social interactions among groups of scavengers. The striated caracara (*Phalcoboenus australis*) is a social scavenging falconid of the Falkland Islands, whose boldness and reliance on human settlements as winter foraging grounds make it an ideal species with which to closely examine carcass use over the entire period of a carcass' availability. By providing and monitoring experimental carcasses, we estimated the mass of food consumed per individual during 5-min intervals and compared the rate of group formation in the presence and absence of conspecific vocalizations. We found (1) that food obtained per individual was greater toward the beginning of carcass availability, when competition was fierce; (2) that vocalizations, by birds at and approaching the carcass, preceded periods of faster group formation; and (3) that on average birds would approach a speaker playing conspecific calls more closely than one playing a control recording. Our observations add to those of social foraging in other scavengers, providing a study of carcass use and vocalization at these ephemeral resources.

## Significance statement

Currently ranked as Near Threatened by BirdLife International, the remote and restricted range of the striated caracara (*Phalcoboenus australis*) has made it a difficult study subject, though conservation concerns show it warrants deeper research. A social scavenging falconid of the Falkland Islands, striated caracaras have been persecuted as livestock pests since the 1800s, but their reliance on human settlements as winter foraging grounds makes them an ideal species with which to examine social scavenging behavior. This study was undertaken to investigate group feeding at carcasses by striated caracaras in austral winter, and to better understand the social function of their vocalizations. Furthering our knowledge of avian vocalizations is essential to certain wildlife management strategies, and empirically testing the effects of playbacks on target species is a crucial prior step to the use of any bio-acoustic tool.

**Keywords** *Phalcoboenus australis* · Gang behavior · Scavenging · Social feeding

## Introduction

The decision to forage in a specific area usually is made to strike a balance between the amount of available food, the amount of competitors for that food, and the amount of predators nearby (Stephens 2008). Although conspecific competitors can result in reduced food availability for the individual forager, many predatory and scavenging species still aggregate around food resources (Rabenold 1987; Heinrich 1988; Diamond and Bond 1991; Heinrich and Marzluff 1995; Kirk and Houston 1995; Marzluff et al. 1996; Stahler et al. 2002; Bickerton and Szathmáry 2011; Dwyer and Cockwell 2011; Kendall et al. 2012). Foraging individuals may lack other options or prefer certain food resources over others; for example, Common Ravens (*Corvus corax*) in a large forest patch

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may choose to forage on the same deer carcass, despite the availability of other foods (Heinrich 1989). Other scavengers may choose to defend the resource and exclude conspecifics (Heinrich and Marzluff 1995; Travaini et al. 1998; Stephens 2008). Why some scavengers gather in large numbers and share the carcass suggests sociality could play a role in food acquisition or discovery for those species.

Group feeding at carcasses has been investigated in detail in vultures in Africa (Houston 1974; Ruxton and Houston 2002; Jackson et al. 2008; Kendall et al. 2012; Kendall 2012), and to a lesser degree in vultures in North and South America (Rabenold 1987; Kirk and Houston 1995; Parker et al. 1995). Rabenold (1987) and Parker et al. (1995) showed that black vultures (*Coragyps atratus*) roosting communally follow one another to carcasses, with successful scavengers recruiting individuals from their roosts. Cooperative foraging behavior also has been observed in the Mountain Caracara (*Phalco boenus megalopterus*), a species in which conspecific individuals work together to turn over stones that have food items beneath (Jones 1999). Although this kind of direct cooperation is not common in raptors, group feeding appears to be an important aspect of the consumption of large carcasses in Old World vultures particularly (Kendall et al. 2012). The concentration of individuals near a carcass logically forces them to choose confrontation or sharing (Bickerton and Szathmáry 2011; Wang et al. 2012).

Social foraging also has been explored in corvids (Order: Passeriformes; Family: Corvidae) which are known to vocally recruit to food resources (Heinrich 1988; Heinrich and Marzluff 1991; Bugnyar et al. 2001; Kondo and Hiraiwa-Hasegawa 2015). The group foraging behavior or “gang behavior” in which juveniles, but not adults, gather in large groups at food resources observed in Common Ravens indicates a status- and age-stratified social structure that is also seen in another non-raptor, the Kea (*Nestor notabilis*) (Heinrich 1988; Diamond and Bond 1999). Additionally, ravens use vocal recruitment to attract other ravens from nearby to the carcass, and have recruitment calls that are readily distinguished from other call types (Heinrich and Marzluff 1991; Heinrich et al. 1993). Social calls have also been shown to coordinate foraging in mammals, especially bats, cetaceans, and primates (Hauser 1996).

Group foraging behavior has also been observed in the Striated Caracara (*Phalco boenus australis*), a social, scavenging falconid endemic to the Falkland Islands and Tierra del Fuego (Ferguson-Lees and Christie 2005). These birds have been and continue to be persecuted as livestock pests, though the population is now protected (Woods 2007; Catry et al. 2008; Woods et al. 2012). Striated caracaras are in general unafraid of people, curious, and opportunistic, traits which put them at odds with sheep farmers on the outlying islands of West Falkland (Meiburg 2006; Rexer-Huber and Bildstein 2013), particularly when the birds prey on newborn lambs and

pregnant ewes (Woods 2007; D. Pole-Evans, personal communication (2014)).

The ecology of the striated caracara is linked heavily to seabird colonies on the Falklands, which serve as their main source of food during the breeding season by providing eggs and young and adult carcasses from which to feed (Strange 1996; Catry et al. 2008). Although the gentoo (*Pygoscelis papua*) and king penguin (*Aptenodytes patagonicus*) colonies persist through the winter in some areas, they are not as large as during austral summer, and numbers of caracaras observed at penguin colony sites in winter are not nearly as large as those in summer (Harrington et al. 2018). In winter, the foraging strategy of these birds changes markedly (Harrington et al. 2018). During May to August when dispersing from their natal areas, striated caracaras concentrate in and around human settlements, feeding on offal, kitchen garbage, livestock feed, and sheep or goose carcasses (Meiburg 2006; Woods et al. 2012; Rexer-Huber and Bildstein 2013). Many, if not most, juvenile and subadult striated caracaras forage in groups during the winter (Dwyer and Cockwell 2011; Rexer-Huber and Bildstein 2013), but to what extent such behavior affects food acquisition has not been thoroughly investigated. The formation of groups may allow juveniles to access or locate rare winter food sources which are otherwise difficult to find or use due to the presence of dominant adults. Considering that mortality is highest for striated caracaras within the first year of life (Woods 2007), it would seem an important survival strategy to have evolved.

The amount of food obtained by an individual scavenger is a useful proxy for measuring the benefits or detriments of group foraging behavior. However, it is difficult to obtain even rough estimates of the quantity of food scavengers consume at a carcass in a natural setting. Scavenger assemblages are most often observed on very heavy, natural carcasses, which cannot be weighed before the start of observations (Frere et al. 1999; Selva et al. 2003; Kendall 2012; but see Moleón et al. 2015). One study looking at scavenger density on bison (*Bison bonasus*) carcasses in Poland visually estimated the weight of a carcass on each day and calculated the amount consumed by dividing the depletion by the number of days over which it took place, assuming a constant rate (Selva et al. 2003). This method relies heavily on the observer’s estimation ability, and the assumption of a constant rate of depletion. Because of the extreme tolerance of striated caracaras to human approach, it is possible to closely examine the rate of carcass consumption at a much finer timescale, measuring carcass weight at brief intervals, and recording the number of scavengers actively feeding during those intervals.

This study was undertaken to understand striated caracara social foraging by quantifying the depletion of small carcasses over the entire period of their availability. We investigate how the size and composition of a group affects the amount of food obtained per individual, and how the juvenile grouping

strategy applies to the winter foraging behavior of striated caracaras as it is known in common ravens, including the apparent recruitment qualities of juvenile vocalizations (Heinrich and Marzluff 1991; Heinrich et al. 1993). We predicted that (1) the amount of food obtained per bird would be greater after a crowd gathers, and less when 1–2 birds control the carcass; and that (2) juvenile, but not adult, vocalizations function as recruitment calls, accelerating the aggregation of birds near the carcass and (3) drawing them closer to the source of the call. Although vocalizations produced at carcasses by juveniles may be advertisements of status, or a variant of the begging call when a bird is prevented from accessing food (Grodzinski and Lotem 2007), we hypothesize it is advantageous for a signaler to advertise a food source vocally, allowing conspecifics and possibly relatives to respond quickly, arriving at the carcass while the greatest amount of meat is still available.

## Methods

### Study area

The Falkland Islands is an archipelago of more than 750 islands between 51°–53°S and 62°–57°W in the South Atlantic Ocean, about 400 km off the coast of South America. The human population (about 2500 individuals in 2018) is concentrated in East Falkland in the town of Stanley, and at the military base at Mount Pleasant (Falkland Islands Government).

Saunders Island is the fourth largest island in the Falklands archipelago and is located in the northwest, covering an area of 132 km<sup>2</sup>. It functions as a sheep farm which is run by David and Suzan Pole-Evans. The main settlement (51° 21' 59" S/60° 05' 13" W) is a collection of buildings on the eastern end of the island. In general, the climate of the Falklands is cool and windy; weather is highly variable day to day, especially on the outlying islands (Klügel 2009). During one austral winter field season on Saunders Island (May–July 2015), daily temperatures averaged 4.5 °C (±2.5 °C, SD), and wind speed was 9.0 kts (±4.5 kts) primarily from the northwest. Saunders Island experienced precipitation on 27 of 54 days measured (50%; of which 78% rain, 22% snow), and some degree of cloud cover on 100% of days.

During austral winter (March–October), the striated caracara population on Saunders Island is approximately 200 individuals, about 70% of which are juveniles (birds in their first or second winter), 18% are subadults (birds in their third or fourth winter), and 12% are adults (birds older than 5 years). This number is estimated from daily censuses of the banded caracara population at the settlement, where approximately 70% of individuals encountered are banded with alphanumeric color bands. Age classes are determined in the field by

plumage, bill, and skin color (Dwyer and Cockwell 2011). Most individuals are found within 1 km of the main settlement, where opportunities for scavenging on offal, kitchen garbage, and other animal feeds are frequent. Birds are sometimes observed following humans out of the settlement on excursions up to 10 km, in groups of 1–5 individuals. Falkland Islands government permits to capture and band striated caracaras are held by KLB.

In addition to striated caracaras, Saunders Island, which is listed by BirdLife International as an Important Bird Area, supports 10,000 pairs of Gentoo Penguins, 6900 pairs of southern rockhopper penguins (*Eudyptes chrysocome*), 12,000 pairs of Magellanic penguins (*Spheniscus magellanicus*), and less than 20 king penguins, as well as 17,000 pairs of black-browed albatrosses (*Thalassarche melanophrys*) (Crofts 2014). Other raptors include turkey vultures (*Cathartes aura*), red-backed hawks (*Geranoaetus polyosoma*), southern caracaras (*Caracara plancus*), and peregrine falcons (*Falco peregrinus*) (Woods and Woods 2006). The largest penguin colony is at an isthmus called the Neck (51° 18' 36" S/60° 14' 11" W) in the northwestern part of the island.

### Measuring carcass consumption

Field seasons were conducted on Saunders Island during austral winters in 2011–2012 and 2014–2015. It was never possible to record data blind because our study involved focal animals in the field. All procedures performed in this study involving animals were in accordance with the ethical standards of the IACUC at Boise State University (IACUC Approval Number 006-AC15-001).

We used whole wild male upland goose (*Chloephaga picta*) and domestic sheep shoulders (*Ovis aries*, hereafter mutton) obtained from David Pole-Evans as carcasses. Goose carcasses weighed 3820 g (±100 g, SE; range 2810–4280 g,  $n = 15$ ), and mutton shoulders weighed an average 2540 g (±200 g; range 1660–3460 g,  $n = 8$ ), for a total of 23 carcasses.

A single carcass was weighed on a digital hanging scale and placed in a field at approximately 13 h00 each day, with at least 48 h between trials. Carcasses were placed on the ground 5 m from a blind, and mutton shoulders were staked down (these quickly became light enough for birds to carry out of view). The carcass was then weighed every 5 min with a digital scale, starting from the placement of the carcass within reach of the birds until sequential readings indicated that food was no longer being removed (<20 g removed between intervals for three sequential measurements). Observations for all carcasses averaged 105 min (±44 min, SD).

The age and time of arrival for each bird that visited the carcass were recorded. The disturbance created by weighing the carcass every 5 min appeared minimal, with birds

returning to feed < 5 s after the carcass was weighed, and most remaining within 0.5 m of the experimenter during the weighing procedure. The possibility existed that “braver” or more disturbance-tolerant individuals would then gain preferential access to the carcasses following each weighing step. This was judged to be not detrimental to the data collection because the focus of this study was group-feeding effects rather than individual feeding. Each time the carcass was weighed, the number and ages of birds actively feeding were documented, as well as those not feeding but within 30 m. Striated caracaras are large, dark-colored birds that are easy to pick out against the landscape, and any birds not within 30 m of the carcass were ignored as they were unlikely to be participating in the group. Vocalizing birds were also identified and noted coincidentally by the observer with a band number if applicable and an age class.

An estimate of the amount of food consumed per bird (hereafter, FCPB) was calculated by dividing the amount of food removed from the carcass over each 5-min interval by the number of birds actively feeding at the end of the interval. The proportion of each age class was determined by dividing the number of juveniles or adults by the total number of birds actively feeding. Subadults were not included in this part of the analysis as single individuals exhibited behaviors and vocalizations consistent with both adult and juvenile types, and we wished to focus here on the differences between the two. We also chose to estimate FCPB, even though our focus was on group feeding, to be able to track the differences in food intake between larger and smaller groups, and groups of different age class compositions.

Descriptive statistics of components of feeding on each carcass type were generated in R (v 3.4.3), including initial carcass mass, discovery time (minutes from start until first individual arrived within 5 m of carcass), birds feeding (maximum number of individuals actively eating during each 5-min interval), percent of carcass consumed, depletion time (minutes from arrival of first individual until end of trial), depletion rate (mass removed from carcass over depletion time), and FCPB. These results were compared between carcass types using Student’s *t* tests. A linear model of carcass mass versus time since the start of the trial was constructed in R to estimate the rate of carcass mass decline. A set of generalized linear models were also constructed using package “AICmodavg” to determine which of the factors measured best explained the variability in FCPB over a given time interval. Factors included time, carcass type, carcass mass, total birds, proportion juveniles, and proportion adults. None of these variables were found to be highly correlated with one another ( $\rho \leq 0.60$ ). Nine models and a null model were constructed to test the hypotheses that the variation in the observed FCPB was best explained by either (1) the total number of birds eating, (2) the proportion of the groups that was adults, or

(3) the proportion of the group that was juveniles, or a combination of the three. The output ranked each of these models according to Akaike’s Information Criterion adjusted for small sample size ( $AIC_c$ ) (Burnham and Andersen 2002).

In order to investigate the rate of accumulation of birds to the area of the carcass during each carcass trial in response to the presence or absence of caracara vocalizations, we analyzed 6 of the 23 total carcasses in which vocalization by birds visiting the carcass was delayed by more than 3 min post discovery. For these six carcasses where vocalization was delayed, two simple linear regressions were applied to the total number of birds present at the carcass over time, using Microsoft Excel v 2013. The first line was fit to the rate of birds accumulating prior to any vocalization, and the second was fit to the rate of accumulation after the first vocalization, until the number of birds present reached a maximum. The  $R^2$  value of all lines fit in this manner was  $\geq 0.85$ . These rates (prior and post vocalization) were compared using a Wilcoxon signed-rank test, and further compared to the accumulation rates of birds at the other 17 trials (where vocalization was within 3 min of discovery) using a Wilcoxon rank-sum test.

### Response to conspecific vocalizations

Recordings were made of striated caracara vocalizations at some of the experimental carcasses, as well as in frequented areas around the settlement, using a Sennheiser unidirectional microphone (frequency response,  $\pm 3$  dB over 0.055–20 kHz) with wind cover mounted on a tripod and placed 2 m from the carcasses, selecting a high pass to reduce wind noise. A Roland R-05 recorder recording in .wav format at a sample rate of 96 kHz was attached to the microphone. Calling individuals were identified coincidentally by the observer by age and band number if applicable.

Six recordings were made over a period of 4 days. An additional control recording was taken of ambient noises, which did not include any striated caracara vocalizations, but did include occasional vocalizations of domestic chickens (*Gallus gallus domesticus*). Each recording was analyzed in the sound-editing program Audacity, v. 2.1.0. A further high pass at 1 kHz was employed to remove any remaining wind noise. Individual vocalizations were separated into juvenile and adult type calls to produce three distinct 10-min audio files of each only adult or juvenile vocalizations. Calls from different individuals were randomized to ensure independence and avoid pseudo-replication. One track of control noise was produced with no effort to reduce wind noise.

Playbacks were conducted every 3 days during the 2014–2015 field seasons, independent of carcass trials, at locations within 1 km or 3 km from the main settlement. TIC

Corporation GS5 Mini Outdoor OmniSpeakers (frequency response,  $\pm 2.5$  dB over 0.04–20 kHz) were used to project sound along with a Lepai LP-2020A+ Class T amplifier with a 12-V battery attachment. Calls were played at 40 dB at 5 m, an auditory estimate as precise decibel measurements in the field were confounded by wind noise. Wind direction was considered before each trial.

Juvenile striated caracaras produce loud, raucous caws, notably near food resources like carcasses (Strange 1996). Adult caracaras (birds in their fifth winter) give vocalizations termed “duets”: both members of the pair begin chirping softly, then eventually let out a series of long screaming caws (Strange 1996). Fledged striated caracaras adopt a hunched posture when calling, with head low to the ground and feathers of the back raised (Fig. 1a). In contrast, the adult calling posture involves the neck bent past a 90° angle with the ground (Fig. 1b). Thus, adult and juvenile calls are readily distinguished from one another by ear as well as by observing the caller.

Eight playback trials of each type (juvenile, adult, and control) occurred once each across 24 trials. The experimenter observed from within 10 m of the speaker, which again did not appear to disturb the caracaras or hinder their approach. A 10-min control period was spent recording the proximity and band numbers of birds already present and of new individuals that came within 30 m of the speaker. Then a pre-selected 10-min recording was turned on. Individuals arriving within 300 m of the speaker during this time were noted, and individuals that had arrived during the 10-min control period were noted again if they moved with respect to the speaker. Distances were estimated using the known length of the speaker cable (5 m), or retroactively using the ruler tool in Google Earth (v. 7.1.2.2041) for longer distances using the location of the speaker and distinct landmarks. When the

recording finished, a final silent 10-min observation period was conducted, during which the movement of birds with respect to the speaker was again noted.

Response during each 10-min interval was measured as (1) the number of birds within 300 m of the speaker and (2) the average movement of birds toward or away from the speaker. Distances ranged from a bird touching or perching on the speaker (0 m) to 300 m. Because trials were conducted under different weather, hunger, or curiosity circumstances of the birds, we separated the average distances before and during each trial for all trials. The average distance of birds during the trial was subtracted from the average before the trial to assign a movement factor that was either positive (toward the speaker) or negative (away from the speaker). This factor was divided by the average number of birds present during the two trial periods to compute an average individual movement factor. A Kruskal-Wallis rank-sum test was used on these movement factors as data did not fit the assumptions of normality.

Broadcasting conspecific vocalizations has long been a survey method for bird species, especially in forested areas where visual detection is difficult (Mosher and Fuller 1996; Rae et al. 2015; Wingert and Benson 2018). It has not been demonstrated that these playbacks have any negative short-term effects on behavior, although they may cause detection inhibition, temporarily decreasing the likelihood of observing present individuals (Crozier et al. 2005).

## Data availability

The datasets generated during and analyzed during the current study are available from the corresponding author on reasonable request.

**Fig. 1** Juvenile “hunched” vocalization posture (a) and adult pair display posture (b). Saunders Island, Falkland Islands, 2015 (photos ARA)



## Results

### Patterns of discovery and feeding

Table 1 compares the means of observations made on the two carcass types. Discovery time, averaging 2.5 min overall, did not significantly differ between carcass types and all carcasses were found by striated caracaras within 18 min of placement. Carcasses were never used by other raptors or scavengers, although 2 carcasses were visited closely by an adult female red-backed hawk, which did not eat from the carcass. A total of 23 carcass trials were conducted and included in this analysis. Eight carcasses (35%) were discovered by a single juvenile caracara, one (4%) by a pair of juveniles, six (26%) by a single subadult, five (22%) by a single adult, one (4%) by a pair of adults, and two (9%) by a pair of mixed ages. Although up to 12 birds were observed eating at any carcass at a given time (mean 4.8), up to 40 could be gathered within 30 m of the carcass. The average proportion of juveniles at all carcasses during any interval was 0.71 ( $\pm 0.01$ , SE), and the proportion of adults was 0.15 ( $\pm 0.01$ ).

The mass of each carcass decreased over time, with the rate of decrease slowing with time (Fig. 2). The average number of birds eating at a carcass also decreased over time, after the initial increase as birds discovered the carcass (Fig. 3).

### Factors influencing FCPB

Of the set of generalized linear models constructed to explain the observed variability in FCPB, the top model indicated that time, the total number of birds, and the proportion of adults best explain the observations (Table 2). No other model came within two AICc units of the top model, and so it was considered alone be representative of the data (Table 3).

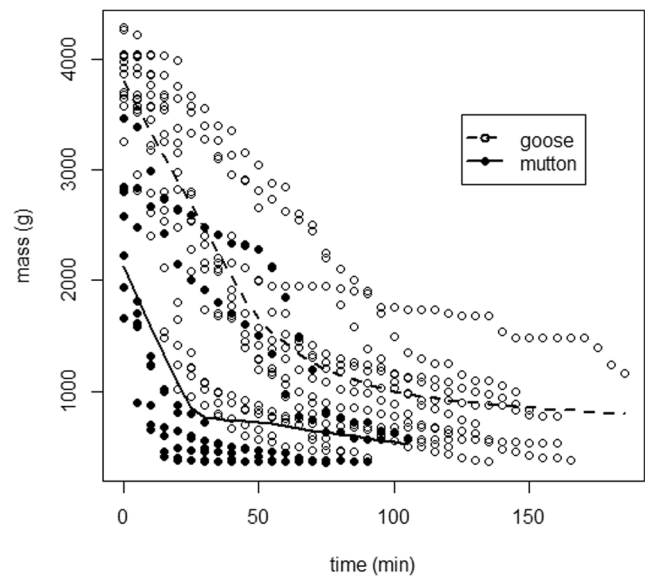
**Table 1** Comparison of observations in both carcass types (means reported with standard errors, *p* value from two-tailed Student's *t* test)

	Goose ( <i>n</i> = 15)	Sheep ( <i>n</i> = 8)	<i>p</i>
Initial mass (g)	3820 ( $\pm 100$ )	2540 ( $\pm 200$ )	< 0.05
Discovery time <sup>a</sup> (min)	3.4 ( $\pm 1.6$ )	0.8 ( $\pm 0.3$ )	0.26
Birds eating <sup>b</sup>	5.1 ( $\pm 0.1$ )	4.2 ( $\pm 0.2$ )	< 0.05
% eaten	82.4 ( $\pm 2.2$ )	83.2 ( $\pm 1.0$ )	0.79
Depletion time (min)	125 ( $\pm 10$ )	65 ( $\pm 10$ )	< 0.05
Depletion rate (g/min)	29.0 ( $\pm 3.3$ )	37.5 ( $\pm 6.3$ )	0.20
FCPB <sup>c</sup> (g/bird)	21.2 ( $\pm 1.3$ )	28.9 ( $\pm 2.5$ )	< 0.05

<sup>a</sup> Minutes from start until first individual arrived within 5 m of carcass

<sup>b</sup> Maximum number of individuals actively eating during each 5-min interval

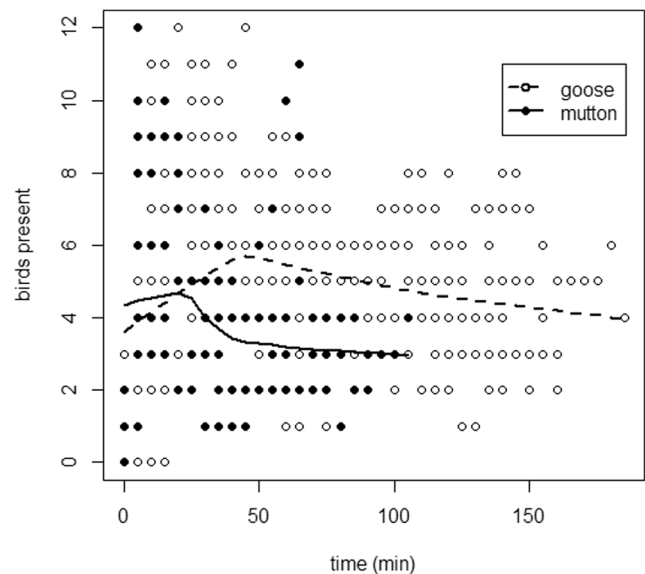
<sup>c</sup> Food consumed per bird (FCPB). Estimated mass of carcass consumed per individual over a 5-min interval



**Fig. 2** Carcass mass versus time for both mutton (*n* = 8) and goose carcasses (*n* = 15). Lines are LOWESS smoothing lines: values determined by linear least squares regression. Simple linear depletion rate averaged 29.0 g/min for goose carcasses, and 37.5 g/min for mutton carcasses (*R* v 3.5.0)

### Vocalizations at carcasses

At five of the 23 total carcasses (22%), the first bird to arrive at the carcass was vocalizing during its approach. Of these signalers, three were juveniles and two were adults. At another six carcasses (26%), birds were actively consuming food for more than 3 min before the first vocalization was emitted, and in these cases four were juveniles, one was a subadult, and one was an adult.



**Fig. 3** Birds present and actively eating goose and mutton carcasses over time. Lines are LOWESS smoothing lines: values determined by linear least squares regression (*R* v 3.5.0)

**Table 2** Summary of top generalized linear model parameter estimates explaining the effect of minutes from start (*time*), number of birds eating (*totbirds*), and the percentage that were adults (*propad*) on food consumed per bird at all carcasses. Adjusted R squared = 0.2972, residual standard error = 22.24

Variables	Model estimate	Standard error	<i>t</i>	<i>p</i>
time	-0.279	0.025	-11.001	<0.0001
totbirds	2.290	0.464	4.932	<0.0001
propad	21.479	4.607	4.662	<0.0001

Birds accumulated near the carcass during these six trials at an average rate of 0.38 birds/min before vocalizations, and at 0.75 birds/min after the initial vocalization. This average was found to be significantly lower before vocalization than after (Wilcoxon signed-rank test,  $V = 21$ ,  $N = 6$ ,  $p = 0.03$ ). The accumulation of birds to carcasses in cases where birds were vocalizing upon or within 3 min of discovery did not differ from the accumulation of birds near the carcass after vocalization for the six instances discussed above (Wilcoxon rank-sum test,  $W = 58$ ,  $N = 6$  and  $17$ ,  $p = 0.66$ ; median = 0.71 birds/min).

### Vocal playback trials

In two of the 24 playback trials (8%), no birds were seen within 300 m of the speaker for the 30-min trial. On average during each period (before, during, and after playbacks) in all trial types,  $6.4 (\pm 4.9 \text{ SD})$  birds were present within 300 m of the speaker when at the settlement,  $5.8 (\pm 4.8)$  birds 1 km from the settlement, and  $1.3 (\pm 1.7)$  birds 3 km from the settlement. The number of birds approaching during each of these trials

**Table 3** Summary of Akaike's Information Criterion adjusted for small sample size (AIC<sub>c</sub>) output on candidate generalized linear model set explaining food consumed per bird (FCPB) ("time" = minutes from start, "birds" = individuals eating, "ad" = proportion adults, "juv" = proportion juveniles, "mass" = carcass (g), "type" = mutton or goose). AICc differences ( $\Delta\text{AICc}$ ), relative weight of models (AICc Wt), log-likelihood (LogLike)

Model	K	AICc	$\Delta\text{AICc}$	AICc Wt	LogLike
time + birds+ad	5	4282.83	0.00	0.96	-2136.35
time + birds+juv	5	4289.05	6.23	0.04	-2139.46
time + birds	4	4302.21	19.38	0.00	-2147.06
time + ad	4	4304.70	21.87	0.00	-2148.31
time + juv	4	4309.88	27.05	0.00	-2150.90
time	3	4320.10	37.27	0.00	-2157.02
mass	3	4361.43	78.60	0.00	-2177.69
birds	3	4404.34	121.52	0.00	-2199.15
type	3	4441.43	158.60	0.00	-2217.69
null	2	4446.57	163.74	0.00	-2221.27

across all periods, however, was not significantly different between trial types:  $4.7 (\pm 4.3)$  birds during adult,  $5.2 (\pm 6.2)$  during juvenile, and  $5.2 (\pm 3.6)$  during control trials (ANOVA,  $df = 2$ ,  $N = 24$ ,  $p = 0.924$ ).

Movement during juvenile and adult trials was significantly different from the movement during control trials (chi-square test,  $\chi^2 = 7.2507$ ,  $df = 4$ ,  $p = 0.03$ ). Individuals moved an average 26 m ( $\pm 14$ ) closer to the speaker when the juvenile track was being played, and 9 m ( $\pm 8$ ) when the adult track was being played, whereas each moved on average 6 m ( $\pm 4$ ) away from the speaker while control tracks were being played.

### Discussion

In agreement with Selva et al. (2003), we found that the mass of a carcass does not decrease at a constant rate, but that the rate of consumption decelerated. This implies that most of the carcass was consumed within an initial period (in this study, roughly 30–50 min), and that it may be advantageous to be among the first birds to arrive at the resource.

Heinrich (1988) found that in Common Ravens (*Corvus corax*), American crows (*Corvus brachyrhynchos*), and blue jays (*Cyanocitta cristata*) carcass discovery occurred by 1 or 2 individuals, but only in common ravens did larger groups subsequently gather. Striated caracaras behaved as ravens did, in that carcasses were found by 1–2 birds, and all were followed by the subsequent aggregation of at least 14 but up to 40 birds.

Our model shows that FCPB is negatively associated with the time from start, and positively associated with the total number of birds eating the carcass, as well as the proportion of adults in the group. This supports the observations that the carcass is depleted over time, but that the subsequent gathering of a large number of conspecifics does not necessarily result in an immediate decrease in food availability and supports the hypothesis that FCPB is greater at the beginning of a carcass's availability.

Increasing the participants at the carcass increases the accessibility of the meat itself may seem counterintuitive. In the absence of native terrestrial mammals, striated caracaras in the Falkland Islands evidently rely on their own morphology to deal with unopened carcasses. However, the large muscle and fat deposits may be made more accessible by having multiple mouths tearing at the carcass from different angles. The arrival of a large amount of birds forces closer contact between those individuals who want to eat, and so two or more birds may end up working together to sever the same tendon, leading to an increased chance that one of them will get that reward, and more quickly, than if they each had been working alone.

Of course, this would not necessarily result in more food for all individuals all of the time. In fact, it was frequently observed that if a large, loosely attached portion of the carcass was removed, such as the legs, head, or gizzard, the bird that

took the piece flew off with it, followed by 3–4 others. This reduced the weight of the carcass considerably, even though the weight of the detached piece was not added to the FCPB of the whole group. We could not accurately reflect these unpredictable events in the model, and so assumed that the removal of the large piece and of the birds that sought it balanced out over the whole trial.

The age composition of groups of striated caracaras that gathered at carcasses did not vary. In our top model, the proportion of adults, not the proportion of juveniles, had the greatest positive effect on FCPB, which implies that adult caracaras may dominate carcasses not only by defending them, but by consuming them quickly. An average of 32.2 g/bird was obtained during 5-min intervals when  $\geq 50\%$  of the group was adults, compared to 22.5 g/bird for intervals with  $\geq 50\%$  juveniles. Although this study was conducted during the winter, adult caracaras, like adult ravens, appear to defend territories from other adults throughout the year, but are far outnumbered by groups of nonbreeding birds (Heinrich and Marzluff 1995).

We failed to show long-distance recruitment to food resources by striated caracara vocalizations, rather demonstrating attractant qualities that may serve to draw in birds that are already present. Several studies with common ravens have shown calling to be an aggregative tool, recruiting others to a site (Heinrich and Marzluff 1991, 1995; Heinrich et al. 1993; Bugnyar et al. 2001). While we hypothesized that grouping was accomplished by the vocalizations of the first arrivals, other mechanisms (i.e., visual) are at work to aggregate birds who were not already aware of the presence of food. Caracaras tended to move toward the source of both types of conspecific vocalizations, and the amount of birds that come to investigate the sound source was not significantly different between treatments and controls. Birds were frequently present during control trials, and there was no significant difference between the number of birds present at any of the trials before or during the experimental playbacks. The difference was instead seen in the distance caracaras were willing to approach the speaker between the control and treatment periods; birds moved closer on average upon hearing both types of conspecific vocalizations, and on average farther away when only hearing control tracks.

In general, if playback trials were conducted in or near the main settlement, birds were attracted to the observer and speaker apparatus regardless of whether any equipment was turned on. The natural curiosity of striated caracaras draws them to novel objects and situations, to perhaps discover food or opportunities for play. Some individuals came near to or followed the observer even during monitoring activities which had never resulted in food “rewards.” Similar to ravens under 6 months of age, juvenile caracaras are quite curious and approach novel objects readily (Heinrich 1995; Miller et al. 2015; Bildstein 2017; Bildstein (2015), unpublished data).

The distance approached to the speaker was not significantly different between adult and juvenile call types, suggesting either that caracaras respond similarly to conspecific vocalizations regardless of their origin or that they do not differentiate between the call types. Both vocalization types may be “parasitized” (i.e., used for the responders benefit against the intentions of the signaler) by hungry birds, or the calls may simply indicate the occurrence of a conflict, likely to be about food.

During the carcass experiments, we also found that vocalizations accelerated the arrival of birds at the carcass. Prior to any type of vocalization, birds probably aggregate because they see the carcass itself, or a small group of caracaras gathered tightly together, but this median rate of aggregation was significantly slower than the rate of birds arriving after the first vocalization has been emitted. Further investigations into the carcass discovering ability of striated caracaras should include testing visual recruitment by itself.

Management of a wild bird that is as curious and adaptive as the striated caracara is a challenge. However, one of the major industries of the Falklands, wildlife tourism, could benefit greatly from increased interest in this near-tame and seemingly intelligent bird. A greater understanding of these birds’ biology and behavior could cascade through the Falklands economy, providing even greater incentives for tourism, and therefore incentives for farmers to protect and maintain habitat for these birds on their land.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflicts of interest.

**Ethical approval** All procedures performed in this study involving animals were in accordance with the ethical standards of the IACUC at Boise State University.

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