GANG BEHAVIOR AT CARCASSES IN WINTERING STRIATED CARACARAS (*Phalcoboenus australis*) IN THE FALKLAND ISLANDS

by

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DEDICATION

For Rhys, in love and gratitude.

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ABSTRACT

Avian scavengers perform vital ecosystem services by removing waste and by slowing disease. Yet few details are known about the purpose or purposes of social interactions near carcasses and their role in the physical depletion of carcasses (Gangoso et al. 2013). The globally Near-Threatened Striated Caracara is a social scavenging falconid that relies on seabird colonies for food during the breeding season in the Falkland Islands, a principal stronghold in its range. The birds have been persecuted as livestock pests since the late 1800s. Although the population is now protected and remains stable, it does not appear to be growing. The caracaras' reliance on human settlements as winter foraging grounds makes them an ideal species to examine age-stratified consumption over the entire period of a carcass's availability. By providing and closely monitoring experimental carcasses, I estimated the mass of food consumed per bird over five minute intervals (mean 22.9 g/bird/5 min, ±1.2, SE), and found that this was negatively influenced by the time of arrival to the carcass, positively by the total numbers of birds feeding on the carcass, and positively by the proportion of the group that was adult birds. I also found that, as previously shown in Common Ravens, aggregation of a group to a carcass can be accelerated by vocalizations of the birds (Heinrich and Marzluff 1995). My data indicate that the so-called gang behavior in juvenile caracaras is very similar to that in ravens, and is an adaptive strategy to overwhelm adults at ephemeral resources and obtain food.

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FPB	"Food per bird". An estimate of the amount of food (in grams) consumed by a single caracara during a measured 5-minute period.

CHAPTER ONE: GANG BEHAVIOR AT CARCASSES BY WINTERING STRIATED CARACARAS

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). A large number of conspecific competitors may result in reduced food availability for the individual forager and induce caching behavior (Heinrich and Pepper 1998). However, many predatory and scavenging species still do aggregate around food resources (Rabenold 1987; Heinrich 1988; Diamond and Bond 1991; Kirk and Houston 1995; Heinrich and Marzluff 1995; Marzluff et al. 1996; Stahler et al. 2002; Bickerton and Szathmáry 2011; Dwyer and Cockwell 2011; Kendall et al. 2012). Foragers may lack other options; for example, all ravens in a large forest patch may choose to forage on the same deer carcass, as it is the only resource available (Wang et al. 2012) and as it offers too much food for smaller numbers of birds. While burying or caching pieces of a large carcasses may be cumbersome, scavengers may also choose to defend the resource and exclude conspecifics (Heinrich and Marzluff 1995; Travaini et al. 1998; Stephens 2008). Why some scavengers choose to gather in large numbers and share the carcass implies sociality plays an important role in food acquisition for those species.

Although group hunting has been well-documented in many species of raptors, group feeding at carcasses has only 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) show that Black Vultures (*Coragyps atratus*) roosting communally learn to follow one another to carcasses, with successful scavengers recruiting individuals from their roosts. Cooperative foraging behavior also has been observed in the Mountain Caracara (*Phalcoboenus megalopterus*), a species in which individuals work together with conspecifics to turn over stones that have food items beneath (Jones 1999). Although this kind of direct cooperation is not common in raptors, social feeding appears to be an important aspect of the consumption of large carcasses. The concentration of individuals near a carcass forces them to choose a confrontation over dominance, or the need to share (Bickerton and Szathmáry 2011; Wang et al. 2012).

Social foraging also has been explored extensively in corvids (Order: Passeriformes; Family: Corvidae), which are known to vocally recruit other 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” observed in Common Ravens (*Corvus corax*) indicates an age-stratified social structure also seen in Keas (*Nestor notabilis*) (Heinrich 1988; Diamond and Bond 1999). Resident adult ravens chase off non-residents or juveniles when non-residents approach a carcass singly. However, when the non-residents gather in large groups, this behavior allows them to access the carcasses and obtain food (Heinrich 1988). Additionally, ravens use vocal recruitment to attract other ravens from nearby to the carcass, and have distinct recruitment calls that are readily distinguished from other call types (Heinrich and

Marzluff 1991; Heinrich et al. 1993). Social calls have even been shown to coordinate foraging in mammals, especially bats, cetaceans, and primates (Hauser 1996).

The Striated Caracara (*Phalcoboenus australis*) is 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, even though the population is now protected (Catry et al. 2008; Woods 2007; 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 weak newborn lambs and pregnant ewes (Woods 2007; David Pole-Evans, pers comm).

The ecology of the Striated Caracara is linked heavily to seabird colonies on the Falklands, which serve as their main source of food by providing eggs, 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 and diverse as during austral summer, and apparently do not provide sufficient resources to sustain the same numbers of caracaras. In winter, the foraging strategy of these birds changes markedly. During May to August, when pushed from their breeding and natal areas, Striated Caracaras concentrate in and around human settlements, feeding on offal, kitchen and other farm garbage, livestock feed, and sheep or goose carcasses (Meiburg 2006; Rexer-Huber and Bildstein 2013; Woods et al. 2012). 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.

Upon discovery of a food source, a single juvenile Striated Caracara may find it already being fed upon by an adult or pair of adults. About 75% of the time, the juvenile begins emitting a loud, rasping call, and within a few minutes other individuals appear. This large group can overwhelm an adult or pair of adults, allowing a larger percentage of the group to feed at a carcass. The formation of these groups or gangs may allow juveniles to access rare winter food sources that are otherwise inaccessible. 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 fitness benefits 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 large, 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 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). These data, accompanied by estimates of the proportion of scavenger species visiting the carcass, allow approximation of the weight of carrion consumed by each species. 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 for the entirety of the carcass's availability.

This study was undertaken to understand the dynamics of social foraging by scavengers by quantifying the depletion of small carcasses over the entire period of their availability. I show how the size and composition of a large group affects the amount of food obtained by each individual, and how the juvenile gang behavior 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). Though the amount of food available to each individual at a carcass presumably is reduced when large groups form, I predicted that (1) the amount of food obtained per bird would be greater when a crowd gathers, and less when 1-2 birds control the carcass, and that (2) juvenile vocalizations function as recruitment calls, accelerating the aggregation of birds near the carcass. I hypothesize it is advantageous to advertise a food source in this way, and to respond by arriving quickly 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 2900 individuals in 2012) is concentrated in East Falkland in the town of Stanley, and at the military base at Mount Pleasant (i.e., Falkland

Islands Government). The Falklands are a British Overseas Territory, and their economy focuses on fishing, oil exploration, wool production, and tourism.

Saunders Island, the fourth largest island in the Falklands archipelago, is in the northwest, with an area of 132 km^2. It functions as a sheep farm run by David and Suzan Pole-Evans, and during austral summer (November-February) provides self-catering cottages for tourists. The main settlement (51°21’59” S/60°05’13” W) is a collection of buildings on the eastern edge of the island (Figure 1.1). 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 the 2015 field season on Saunders Island (May-July), 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 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.

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, 6,900 pairs of Southern Rockhopper Penguins (*Eudyptes chrysocome)*, 12,000 pairs of Magellanic Penguins (*Spheniscus magellanicus)*, and less than 50 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 polysoma*), 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 winter 2014 (28 July – 8 August) and late autumn through winter 2015 (18 May – 16 July). Experimental feeding trials also were conducted by K. Bildstein, K. Rexer-Huber, and D. Barber in autumn and winter 2011 and 2012. The permits to capture and band Striated Caracaras on the Falkland Islands are held by K. Bildstein.

I used whole wild male Upland Goose (*Chloephaga picta*) and mutton shoulders (*Ovis aries*) obtained from David Pole-Evans as carcasses. Goose carcasses weighed on average 3820g (± 100g, SE; range 2810g-4280g, n=15), and mutton shoulders weighed an average 2540g (± 200g; range: 1660g-3460g, n=8).

A carcass was weighed and placed outside at approximately 13h00 each day, with at least 48 hours between trials. Mutton, but not goose carcasses, were staked into the ground 5m from the observation post, as mutton carcasses quickly became light enough for birds to carry out of view, and goose rarely did (Figure 1.1). The carcass was weighed every five minutes 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. Observations for all carcasses averaged 105 minutes (± 9 minutes).

The age and time of arrival for each bird that visited the carcass were recorded. The disturbance created by weighing the carcass every five minutes appeared minimal, as birds returned to feeding <5 seconds after the carcass was replaced, and most remained within 0.5 m of the experimenter. Each time the carcass was weighed, the number of birds actively eating (on) was documented, as well as those within 30 m (off), and their ages. Vocalizing birds were also identified, and noted with a timestamp. Striated

Caracaras are easy to visually place in three age categories: juvenile (first-second winter), subadult (third-fourth winter), and adult (fifth winter) by differences in plumage, bill, and skin color (Dwyer and Cockwell 2011).

An estimate of food per bird (hereafter, FPB) was calculated by dividing the amount of food removed from the carcass over each five minute interval by the number of birds actively feeding at the end of the interval. The proportion of juveniles and the proportion of adults also was determined by dividing the number of juveniles or adults by the total number of birds actively feeding.

Pig-Pen Observations

The proximity of juvenile, subadult, and adult caracaras to a food source when confronted with heavy competition were investigated during the winters of 2011, 2012, 2013, and 2014. Six times each week, at approximately 15h00, an Upland Goose carcass was fed to two pigs in a pen in the settlement (Figure 1.1, Figure 1.2). A majority of the caracaras present in the settlement during the day gather at the pig pen at this time and try to take bits of goose away from the pigs. The pigs themselves pose a low level threat to the birds, and so only a few birds are present inside the pen at a given time. These inside birds, however, also have the greatest potential for reward. Some birds stand on the pen’s railing, and some stand on the ground outside of the pen, providing clear divisions in distance from the food that are more easily quantified than during the carcass experiments.

At the beginning of feeding, the numbers of birds of each age class at each location (inside, railing, and outside) were recorded. These same observations were then taken every five minutes until the carcass was consumed entirely by the pigs, or became otherwise inaccessible to the birds. Sixteen of these trials were conducted and the length of the trials averaged 45 minutes (± 4 minutes).

Results

Feeding on Carcasses – Upland Goose

Of the 23 carcasses, 15 (65%) were Upland Goose. Discovery time averaged 3.4 minutes (± 1.6). Twelve (80%) were discovered by at least one bird within 2 minutes of carcass availability, and all were discovered within 18 minutes. Six (40%) were discovered by a single juvenile, 3 (20%) were discovered by a single adult, 5 (33%) were discovered by a single subadult, and 1 (7%) was discovered by a group consisting of 1 subadult and 1 juvenile.

The average initial mass of goose carcasses was 3820g (± 100g), which decreased over time (Figure 1.3). A simple linear model constructed in R v 3.1.1. estimated the rate of this decline averaged 29.0 g/min (± 3.3), however it should be noted the rate of mass decrease slowed over time (Figure 1.3). The average number of birds actively eating at the carcass during a given interval was greater at goose carcasses, at 5.1 birds (± 0.1), and it too decreased over time, after an initial increase as birds discovered the carcass (Figure 1.4). Upland Goose carcasses took longer to fully deplete than mutton, on average lasting 125 minutes (± 10), and reaching a percent depletion of the total initial mass of 82.4% (± 2.2). Mean FPB on all goose carcasses was 21.2 g/bird (± 1.3), and decreased over time (Figure 1.5, Table 1.I).

Feeding on Carcasses - Mutton

Of the 23 carcasses, 8 (35%) were skinned mutton shoulders. All 8 were discovered by at least one bird within the first 2 minutes of carcass availability.

Discovery time averaged 0.8 minutes (± 0.3). Two were discovered by a single juvenile, 1 by a pair of juveniles, 2 were discovered by a single adult, 1 by a pair of adults, 1 by a single subadult, and 1 was discovered by 1 adult and 1 juvenile.

The average initial mass of mutton shoulder carcasses was 2540g (± 200), and the average number of birds eating at the carcass during a given interval was 4.2 birds (± 0.2), both of which decreased over time (Figures 1.3 and 1.4). The same model described for goose carcasses was used to show that the rate of depletion for mutton carcasses was 37.5 g/min (± 6.3). Mutton carcasses were depleted fairly quickly, lasting on average 65 minutes (± 10) and reaching a percent depletion of the total initial mass of 83.2% (± 1.0). Mean food per bird (FPB) on all mutton carcasses was 28.9 g/bird (± 2.5), and it too decreased over time (Figure 1.5, Table 1.I).

Factors Influencing FPB

A set of generalized linear models were constructed in R using package ‘AICmodavg’ to determine which of the factors measured best explains the variability in FPB over a given time interval (R Core Team 2014). FPB was regressed against time, carcass type, carcass mass, total birds, the proportion of juveniles, and the proportion of adults. None of these variables were found to be highly correlated with each other ($\rho \leq 0.60$). Nine models and a null model were constructed to test the hypotheses that the observed FPB was best explained by either (1) the total 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 (AIC_c) adjusted for small sample size (Burnham and Anderson 2002). No model came within two AICc units of the top model, and so it was considered alone (see output in Table 1.II).

The results of the model indicate that time, the total number of birds, and the proportion of adults best explain the observed variability in FPB (Table 1.III). As the mass of the carcass decreases over time, birds obtain more FPB if they are present when the carcass has its greatest mass. FPB was also positively associated with the number of birds present at the carcass; FPB is shown to increase with an increasing number of birds actively eating the carcass. Finally, the model shows a positive relationship between FPB and the proportion of adults near the carcass.

Vocalizations

At 5 of the carcasses (22%), the first bird to arrive at the carcass was vocalizing during its approach. In an additional 6 carcasses (26%), birds were actively consuming food for more than 3 minutes before the first vocalization was emitted. For the 6 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 accumulation of birds prior to any vocalization, and the second was fit to the accumulation of birds 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 ≥ 0.85.

The median accumulation of birds near the carcass during these 6 trials was 0.38 birds/min before vocalization, and 0.75 birds/min after the first vocalization. Using a Wilcoxon signed-rank test, this rate is shown to be significantly slower before vocalization than after ($V = 21$, $p = 0.03$). The accumulation of birds in those cases where birds were vocalizing upon or within 3 minutes of the discovery of the carcass did not differ from the accumulation of birds near the carcass after vocalization for the 6 instances discussed above (W = 58, p = 0.66; median = 0.71 birds/min).

Age Class Interactions

Group age-class composition did not vary widely, with the average proportion of juveniles at all carcasses during any interval averaging 0.71 (± 0.01), and the proportion of adults averaging 0.15 (± 0.01).

This was very similar at the pig pen, where the proportion of juveniles at any given time was 0.69 (± 0.01) and adults was 0.13 (± 0.01). The proportions of juvenile and adult birds that were either inside, on the railing, or outside the pig pen were also similar to each other. On average during a count interval, 33% (± 2%) of juveniles were inside, 23% (± 2%) were on the railing, and 44% (± 2%) were outside. Considering adults, 32% (± 3) were on average inside, 21% (± 3%) were on the railing, and 47% (± 3%) were outside. Combining all age classes, 34% of birds were on the inside, 23% were on the railing, and 43% were on the outside of the pig pen during a given count. We did not track the movements of individual birds among the three areas.

Discussion

Carcasses provide scavengers with high but infrequent quantities of essential nutrients. Naturally, when a carcass is exposed to scavengers, it decreases in weight until no more nutrients can be gained. In agreement with Selva et al. (2003), I found that the weight of a carcass does not decrease at a constant rate, but that the rate of consumption decelerates: mass falls off steeply for an initial period, followed by a period of slower consumption (Figure 1.3). This implies that most of the edible parts of the carcass are consumed within this (in this study, 30-60 minute) period, and that it is advantageous to be among the first discoverers.

We expect scavengers have at least three choices upon discovery of a carcass: to hide or cache it, to defend it, or to share it. I argue that the strategy employed by wintering juvenile Striated Caracaras is to tolerate the presence of other juveniles in order to form a gang and overwhelm defensive adults, similar to behavior observed in Common Ravens (Heinrich and Marzluff 1995). Using FPB as a proxy for fitness, I show that this gang behavior, evidenced by the rapid aggregation of birds near a carcass and frequent vocalization, is directly advantageous to birds that participate by increasing their access to the food.

Heinrich (1988) found that in three species of corvids, carcass discovery was accomplished by 1 or 2 individuals, but only in ravens did large groups subsequently gather. Striated Caracaras would seem to follow the raven model, as all carcasses in this study were discovered by 1 (n=19), 2 (n=3), or 3 (n=1) birds, and all were followed by the subsequent aggregation of at least 14 but up to 40 birds. The number of birds able to simultaneously feed on the carcass was never more than 12, however (Figure 1.4).

In many studies of carcass utilization, scavengers return to the same large carcass for multiple days, as the resource cannot be fully depleted in minutes or hours (Selva et al. 2003, Moleón et al. 2015, but see Travaini et al. 1998). Thus recruitment to a carcass may involve information sharing at roosts as shown in black vultures and ravens (Rabenold 1987, Marzluff et al. 1996). As the average depletion time for all carcasses in this study was only 105 minutes (1.8 hours), caracaras should use a more immediate mechanism to attract group members to a carcass, such as a visual or auditory cue.

Several studies have investigated auditory behavior in ravens, and have shown calling to be an aggregative tool, attracting others to the site (Heinrich and Marzluff 1991, Heinrich et al. 1993, Heinrich and Marzluff 1995, Bugnyar et al. 2001).

During the carcass experiments, I also found vocalization caused an acceleration in the number of birds arriving near a carcass. Prior to any type of vocalization, birds probably aggregate because they saw the carcass itself, or a small group of caracaras gathered tightly together, but this median rate of aggregation was 0.38 birds/min, significantly slower than the rate of birds that arrive after the first vocalization has been emitted, a median of 0.75 birds/min. Despite the small sample size, this suggests that although birds are initially drawn toward the carcass by visual cues, auditory cues accelerate this process by alerting birds to resources not necessarily in their sphere of activity. Again like juvenile ravens, juvenile caracaras are naturally curious and approach novel objects readily (Heinrich 1995, Miller et al. 2015, K. Bildstein, unpublished data). Frequent high winds reduce the distance over which sound can propagate in West Falkland, and so auditory cues, while important for concentrating groups already loosely aggregated, are evidently not the sole mechanism for carcass recruitment. Further investigations into the carcass discovering ability of Striated Caracaras should include testing visual recruitment.

Nonetheless, it is somewhat counterintuitive that increasing the number of individuals sharing a resource would result in a greater portion of that resource for each individual. The model shows that FPB is positively associated with the total number of birds eating the carcass, as well as the proportion of adults in the group, and the time of arrival. Figure 1.6 illustrates the trends both in total number of birds and FPB over time, averaged across all carcasses. The two lines appear directly proportional over the first 30-50 minutes of carcass availability, but as the carcass is depleted they become inverse (i.e., the more birds eating a *depleted* carcass, the less each gets).

One explanation for the initial proportional relationship is that increasing the participants at the carcass increases the accessibility of the meat itself. Heinrich (1989) hypothesized that ravens call out upon discovery of a carcass to attract mammalian “carcass openers” such as bears, wolves, or coyotes, whose large teeth and strong jaw muscles are better equipped to tear through tough hides than a raven’s beak. In the wild, ravens are known to associate with hunting packs of wolves to snatch a bite from the pack’s kill (Stahler et al. 2002). 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 ultimately had the piece in its mouth flew away, followed by 3-4 competitors (A. Autilio, observations). This dramatically reduced the weight of the carcass during the next interval, but the weight of the detached piece cannot be said to have added to the FPB of the whole group.

The fact that greater FPB was obtained from mutton carcasses than goose carcasses does not necessarily reflect a trend of more birds present at the mutton. In fact, the opposite was found (Table 1.I). An important difference between the two types were that mutton carcasses were skinned, so muscle and fat tissue were fully exposed at the beginning of each trial. The goose carcasses were whole and feathered, requiring birds to spend some time plucking and breaking through the skin. Although birds routinely demonstrated strategies to make breaking into a goose carcass more efficient (starting from the vent, removing the eyes or tongue) on the whole, mutton carcasses were depleted sooner and more FPB was obtained from them. Future investigations should present plucked or skinned goose carcasses to compare rates of depletion.

The age composition of groups of Striated Caracaras that gathered near carcasses did not change in response to vocalizations, and was no different from groups seen distributed around the settlement. Age class also did not appear to have a large effect on the proximity of birds to the carcass during pig pen trials. The proportions of adults and juveniles that were inside, on the railing of, or outside the pig pen during feeding were not significantly different from one another, suggesting that gang behavior equalizes the playing field, allowing juveniles to compete successfully with more aggressive adults. However, the pigs themselves may have limited the accessibility of the area inside the pen and the food source, further complicating which birds were inclined to enter the pen. In the top model, the proportion of adults, not the proportion of juveniles, had the greatest positive effect on FPB, which demonstrates that adult caracaras dominate carcasses not only by defending them, but by consuming them quickly. An average of 32.2 g/bird was obtained during 5-minute intervals when ≥ 50% of the group was adults, compared to

22.5 g/bird for intervals with ≥ 50% juveniles. Although this study was conducted during the winter, adult caracaras, like adult ravens, appear to have individual distances throughout the year, but are far outnumbered by groups of nonbreeding birds (Heinrich and Marzluff 1995).

Management of a wild bird that is as curious and adaptive as the Striated Caracara is a challenge. They learn very quickly what is and what has the potential to be rewarding, and interfering with farming activities is a popular pastime. 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. Nearly all photographers and eco-tourists who come to the Falklands to get up-close views of penguin colonies and seal rookeries will come into contact with the Striated Caracara, whether they intended to or not. 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.

CHAPTER TWO: RESPONSE TO CONSPECIFIC VOCALIZATIONS

Introduction

As signals to conspecifics, animal vocalizations can communicate a threat, a warning, a submission, or a solicitation (Bradbury and Vehrencamp 2011). In most instances, a predator or scavenger should want to keep an ephemeral resource like a carcass hidden from competitors, in order to obtain the most food from it; for example, by caching pieces of a carcass out of view of others (Heinrich and Pepper 1998). However, social feeding occurs in a variety of raptors species, including scavengers like the Turkey Vulture (Kirk and Houston 1995) and Black Vulture (Parker et al. 1995). These two species do not have extensive vocal capabilities however, and social coordination likely happens as result of movement near roost sites (Rabenold 1987).

Juveniles Striated Caracaras (birds in their first and second winter) produce loud, raucous caws (Strange 1996) in a call that resembles the European Rook's (*Corvus frugilegus*). Juvenile caracaras fully develop their call by March of their first year, late into their first austral summer, and some individuals are more vociferous than others. Birds in their first 6 months and females are disproportionately the most vocal individuals (Strange 1996). The juvenile call is probably directly derived from the nestling food-begging call that is usually rewarded by a responsive parent (Grodzinski and Lotem 2007).

The adult (birds in their fifth winter) vocalization is termed a "duet": both members of the pair begin chirping softly, until they reach a climax in which they throw back their heads and let out a series of long screaming caws. Adult Striated Caracaras are not thought to vocalize as often as juvenile birds, instead using their duets to defend against invaders, or when they have obtained a food item (Strange 1996). Dueting may be directed at the other member of pair, as during mating season and courtship, copulation, and gathering of nest materials, to solidify the pair bond, or toward intruding birds when a pair is defending an area of use (Strange 1996).

Subadult caracaras, third or fourth winter birds who have not molted fully into adult plumage, sometimes switch back and forth between these two call types, as was observed with banded individuals during the 2015 field season on Saunders Island (A. Autilio, observations).

Juvenile Striated Caracaras also adopt a hunched posture when calling, with head low to the ground and feathers of the back raised (Figure 2.1a). Juveniles may also adopt a similar posture when they have obtained an advantageous position near a carcass, and hold the food down with one foot while lifting the head into the air and calling. This is different from the adult calling posture, as adults bend their necks past a 90° angle with the ground, calling at the highest point in this arc (Figure 2.1b). A similar pairing of vocalization to physical posture is reported for adult and juvenile Common Ravens (*Corvus corax*) (Heinrich 1989).

Vocal recruitment has been investigated thoroughly in Common Ravens in North America and Europe. Heinrich (1989) found with numerous experiments involving Common Ravens that playbacks of yelling vocalizations are effective at attracting ravens who are already aggregated in an area to a food bonanza nearby. Heinrich et al. (1993) found that more birds were attracted to small groups near a carcass than to groups that were already quite large, and that ravens preferred to move toward recordings of begging juvenile vocalizations than confront dominant adults. The yelling call was deemed recruitment, as it increased the signaler's fitness by allowing the large crowd of birds thus gathered to neutralize the defenses of adults (Heinrich and Marzluff 1991). However, all three studies note that vocal recruitment is just one of a variety of mechanisms that induce the formation of large groups at food bonanzas. Heinrich and Marzluff (1991) argue that while the ultimate goal of recruitment is the attraction of a group to a large resource, yells are proximally released by hunger and may also function as expression of status. The correlation between dominance status and calling rate also was demonstrated by Kondo and Hiraiwa-Hasegawa (2015) in the Large-billed Crow (*Corvus macrorhynchos*).

Raven populations often contain a few dominant individuals that vocalize more frequently than the majority of others, and may even suppress the vocalizations of less dominant individuals by chasing them off (Heinrich 1988, Heinrich and Marzluff 1991). Of the Striated Caracaras observed at carcasses during this study, only a handful were known to vocalize (33 (19%) out of 172 banded individuals seen during 2015 season, and 11 (6%) of those to do so consistently, sometimes for 40 minutes at a time). In Common Ravens in Poland, calling rate near a carcass decreased over time, presumably as the carcass was depleted (Bugnyar et al. 2001).

Broadcasting conspecific or heterospecific vocalizations has long been a survey method for bird species, especially in densely forested areas where visual detection is difficult (Mosher and Fuller 1996, Rae et al. 2015). It has not been demonstrated that these playbacks have any negative short-term effects on behavior, although the perception of conspecific calls by very agressive birds may cause short-term detection inhibition, as was found with Spotted Owls (*Strix occidentalis*) (Crozier et al. 2005).

The previous study (Chapter 1) demonstrated that juvenile Striated Caracaras obtain the most food from a carcass if they are among the first to arrive, and if they are present in a large group of other juveniles, in order to outcompete the more dominant adults. I hypothesized that the vocalizations emitted by certain juveniles function to recruit others from the area to the carcass resource, thereby increasing the number of juveniles at the carcass and overwhelming adults. I predicted that by broadcasting juvenile vocalizations from a speaker in the absence of an obvious food source, juveniles would 1) aggregate to the speaker and 2) approach the speaker more closely than they would around a speaker that was broadcasting a control, wind-noise recording. In this study, I tested the effects of playbacks of conspecific vocalizations on the number and approach distance of Striated Caracaras to the sound source, in order to replicate experimentally the apparent vocal recruitment of individuals to carcass resources.

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 2900 individuals in 2012) is concentrated in East Falkland in the town of Stanley, and at the military base at Mount Pleasant (i.e., Falkland Islands Government). The Falklands are a British Overseas Territory, and their economy focuses on fishing, oil exploration, wool production, and tourism.

Saunders Island, the fourth largest island in the Falklands archipelago, is in the northwest, with an area of 132 km^2. It functions as a sheep farm run by David and Suzan Pole-Evans, and during austral summer (November-February) provides self-catering cottages for tourists. The main settlement (51°21’59” S/60°05’13” W) is a collection of buildings on the eastern edge of the island (Figure 1.1). 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 the 2015 field season on Saunders Island (May-July), daily temperatures averaged 4.5°C (± 2.5°C, SD), and wind speed was 9.0 kts (± 4.5 kts, SD) primarily from the northwest. Saunders 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.

In addition to Striated Caracaras, Saunders Island, which is listed by BirdLife International as an Important Bird Area, supports 10000 pairs of Gentoo Penguins, 6900 pairs of Southern Rockhopper Penguins (*Eudyptes chrysocome)*, 12000 pairs of Magellanic Penguins (*Spheniscus magellanicus)*, and less than 50 King Penguins, as well as 17000 pairs of Black-browed Albatrosses (*Thalassarche melanophrys)* (Crofts 2014). Other raptors include Turkey Vultures (*Cathartes aura*), Red-backed Hawks (*Geranoaetus polysoma*), 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.

Response to Conspecific Vocalization Experiment

Recordings were made of caracara vocalizations at experimental carcasses and at a pig pen during pig feeding. Six times each week, at approximately 15:00, an Upland Goose carcass is fed to two pigs being raised for meat in a pen in the settlement (Figure 1.1, Figure 1.2). A majority of the caracaras (30-70 birds) present in the settlement during the day gather at the pig pen during this time and try to snatch bits of goose away from the pigs. A Sennheiser unidirectional microphone (frequency response: ± 3 dB over 0.055 kHz – 20 kHz) with windcover was mounted on a tripod and placed 2-3 m from the greatest density of birds, using a high pass on the microphone's settings in order to reduce wind noise. The microphone was connected to a Roland R-05 recorder that was kept in a waterproof bag, recording in .wav format at a sample rate of 96 kHz. During the recording, the individual vocalizing was identified and a time stamp associated with them in the observer's notes. Many of the vocalizations were made by unbanded juveniles, but most recordings included a few calls by known individuals.

Six vocalization recordings were made over a period of four days. An additional control recording was taken of ambient noises around the settlement, which did not include any caracara vocalizations. This was done to differentiate the caracaras' response to any noisy, foreign object from the response to conspecific-produced sounds. Each of these recordings was analyzed in the sound-editing program Audacity, v. 2.1.0. A further high pass filter at 1 kHz was employed to remove any remaining wind noise. Individual vocalizations were identified within the recording and separated into juvenile and adult type calls to produce three distinct ten-minute audio files of only adult vocalizations and three of only juvenile vocalizations. Calls from different individuals were randomized, and placed at about 4 vocalizations per minute, to ensure independence and avoid pseudo-replication. One track of control noise was also made, with no effort to reduce wind noise.

Playbacks of these vocalizations were performed roughly every three days. TIC Corporation GS5 Mini Outdoor OmniSpeakers (frequency response: ± 2.5 dB over 0.04 kHz – 20 kHz) with 5 m cables were used to project sound, along with a Lepai LP-2020A+ Class T amplifier with a 12 V battery attachment. The same Roland R-05 recorder that collected the recordings was used to play back each track at the volume at which it was recorded. This volume was estimated auditorily to be 40 dB at 5 m, as precise decibel measurements in the field were confounded by wind noise.

Locations within the farm settlement, 1 km and 3 km from the center of the settlement, were chosen for the trial sites. Wind direction and speed were considered before each trial in order to maximize sound projection toward a known concentration of caracaras. Days of intense precipitation were also avoided, and the analysis of one trial was eliminated due to extreme fog, which reduced detectability of birds.

Eight playback trials of each type (juvenile, adult, and control) were planned at varying distance from the settlement for a total of 24 trials. The experimenter observed from within 10 m of the speaker, noting the proximity (m) and age of any birds that were already present. A 10-minute control period was spent recording the ages, proximity, and band numbers of new individuals that came within 300 m of the speaker before recordings were played. This period was necessary to determine whether birds were attracted merely to a novel object (the speaker) or a known curiosity (the experimenter), and not necessarily the recordings.

After this 10-minute period, the pre-selected recording was turned on. Individuals arriving near the speaker during this time were noted by proximity, age, and band number. Individuals that had arrived during the ten-minute control period were noted again if they moved closer to or farther away from the speaker. The distances were estimated using the known length of the speaker cable (5 m), or retroactive analysis using Google Earth (v. 7.1.2.2041), and individuals observed touching or perching on the speaker were recorded at 0 m.

When the recording finished, a final ten-minute observation period was conducted. Again, individuals who arrived near the speaker were recorded, and it was noted if individuals left the area entirely. “Response” to the different playback types during each 10-minute interval was measured as 1) the number of birds within 300 m of the speaker and 2) the average distance of birds to the speaker.

The primary measurement I used to note birds’ interest in the playbacks was the distance each individual approached the speaker. Distance ranged from a bird touching or perching on the speaker (0 m) to 300 m, the limit of my view in most cases. I constructed a generalized linear model with a logarithmic link, fitting the data to the Poisson distribution, using R (R Core Team 2014). The distance of individual birds during the 10-minute treatment portion of each trial was regressed against the independent variables of site of the trial (0, 1, and 3 km from the settlement) and treatment type (adult, juvenile, and control tracks) (Table 2.I).

When blocking for trial site, there were significant differences in the average distance birds approached during each trial type. The mean distance approached by birds during the adult vocalization playbacks was 57.8 m (± 14.3, SE), during juvenile playbacks was 69.4 m (± 12.9), and during control tracks was 83.5 m (± 14.4) (Figure 2.2). The actual number of birds approaching during each of these trials was not significantly different, however: 5.4 (± 1.7) birds during adult, 6.0 (± 2.4) during juvenile, and 4.9 (± 1.4) during control trials (Figure 2.3).

I then compared movement of birds between the initial control and treatment periods of each trial. Because the trials were conducted under different unique circumstances in weather, and hunger or curiosity levels of the birds, I wanted to separate the average distance of birds before and during each trial for all trials. To do this, the average distance of all birds was calculated for each period of each trial (Figure 2.2). Then the average distance of birds during the trial was subtracted from the average distance before the trial to assign a movement factor that was either positive (movement toward the speaker) or negative (movement away from the speaker). I next divided this movement factor by the average number of birds present during those two periods in each trial to compute an average distance each individual moved closer to or farther away from the speaker (Figure 2.4). Because the data did not fit the assumptions of normality, a Kruskal-Wallis rank-sum test was used on the movement factors for all three trial types.

Results

In general, if playback trials were conducted in or very near the settlement, birds were attracted to the observer and speaker apparatus regardless of whether or not any of the equipment was turned on and playing a recording. The natural curiosity of Striated Caracaras draws them to novel objects, activities, and situations, to perhaps discover food or opportunities for play. Certain individuals came near to or followed the observer even when a food reward could not be anticipated, such as the observer walking around the edges of the settlement, or driving an ATV away from the settlement, activities which never resulted in food rewards for nearby birds.

In 2 of the 24 playback trials (8%), no birds were seen in the vicinity of the speaker. Both of those trials were conducted 3 km from the settlement, where the density of birds is generally reduced during the winter months (K. Bildstein, pers. comm.). During all trial periods in all trial types, 6.1 (± 0.9) birds were present during a given trial period within the settlement (0 km), 5.9 (± 1.1) birds were present 1 km from the settlement, and only 1.4 (± 0.4) birds were present per time period 3 km from the settlement.

Movement during juvenile and adult trials was significantly different from the movement during control trials (Kruskal-Wallis $X^2 = 7.2507$, $p= 0.02664$). Each individual moved an average of 26 m (± 14) closer to the speaker when the juvenile track was being played, and 9 m (± 8) when the adult track was being played, whereas each individual moved on average 6 m (± 4) away from the speaker while control trials were being played (Figure 2.4).

Birds within view at the trial sites but that were >50 m away from the observer sometimes were difficult to age. Thus only about 45% of birds counted at trial sites were recorded with ages, and those tended to be the birds that approached the speaker closely. I determined the proportion that were adults, subadults, and juveniles attending each trial type. At all playback trials, a greater proportion of birds were adults than those birds at the carcass and pig pen gatherings (Chapter 1), which was accompanied by a decrease in the proportion of juveniles. The difference, however, was found to be insignificant using a X^2 test where the expected values were those of the age classes at carcass trials (p = 0.94).

Discussion

Having discovered a carcass, a Striated Caracara has two choices: to remain silent, keeping the knowledge of the food isolated yet only obtaining small chunks of meat over a long period of time, or to call out, signaling to conspecifics with whom the discoverer will have to share, but increasing the potential for large rewards (Chapter 1). With this benefit of group foraging in mind, it is possible to envision the adaptive quality of the juvenile begging/advertisement call, and why emitting and responding to such a call has persisted in this population.

The results from these experiments show that caracaras tended to move toward the source of both juvenile and adult vocalizations, even if food was not present, but that the actual amount of birds that came to investigate the sound source was not significantly different between treatment and controls. Birds were frequently present during control trials and the 10-minute periods of control before the experimental tracks, and there was no significant difference between the number of birds present at any of the trials before or during the experimental playbacks (Figure 2.4). 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 conspecific vocalizations, whether juvenile or adult, and on average farther away when only hearing wind noise.

Thus this particular study failed to show the recruitment qualities of Striated Caracara vocalizations, rather demonstrating attractant qualities that served to draw in birds that were already present. Several studies have investigated auditory behavior in ravens, and have shown calling to be an aggregative tool, recruiting others to the site (Heinrich and Marzluff 1991, Heinrich et al. 1993, Heinrich and Marzluff 1995, Bugnyar et al. 2001). While I hypothesized that grouping was accomplished by the vocalizations of the first discoverers, evidently other mechanisms (i.e., visual) are at work to aggregate birds who were not already aware of the presence of food. Frequent high winds reduce the distance over which sound can propagate in West Falkland (Klüger 2009), and so auditory cues, while important for concentrating groups, cannot be the sole mechanism for carcass recruitment.

As argued in the previous chapter, the strategy employed by wintering juvenile Striated Caracaras is to tolerate the presence of others in order to form a gang and overwhelm adults, similar to behavior observed in Common Ravens (Heinrich and Marzluff 1995). Heinrich (1988) found that in three species of corvids, carcass discovery was accomplished by 1 or 2 individuals, but only in ravens did large groups subsequently gather. Striated Caracaras would seem to follow the raven model, as all carcasses in this study were discovered by 1 (n=19), 2 (n=3), or 3 (n=1) birds, and all were followed by the subsequent aggregation of at least 14 but up to 40 birds. Presumably, birds that move closest to an object of potential interest also have the greatest chance of benefiting from the object. If it is a food source, then those birds that respond quickly and accurately to any vocalization in reference to the food source should obtain the most food. Again, my data from the previous chapter show that carcasses are depleted most efficiently in their first 30-60 minutes of availability, and so it is advantageous to be among the first discoverers, or to at least listen and respond quickly.

It should be noted that the distance approached to the speaker by birds was not significantly different between adult and juvenile call types, suggesting that caracaras respond in a similar way to conspecific vocalizations regardless of their origin. A more likely explanation is that both vocalization types are parasitized by hungry birds, and that the calls proximally indicate the occurrence of a conflict, which is likely to be on the subject of food. It is therefore advantageous to investigate any loud, consistent conspecific sound.

Further investigations into the carcass discovering ability of Striated Caracaras should include testing this apparent visual recruitment. Like juvenile ravens, juvenile caracaras are naturally curious and approach novel objects readily (Heinrich 1995, Miller et al. 2015, K. Bildstein, unpublished data). Neophilia may have played a part in the number of birds investigating the experimental speaker apparatus, as these birds have adapted to living closely with humans, and new activities or objects may be potentially rewarding. The green, omnidirectional speaker was not something the caracaras in this study could ever have encountered before, and to a certain degree pure curiosity, rather than the vocalizations, may have contributed to the response of the birds, especially during the control trials.

Furthering our knowledge of bird vocalizations, including their purpose and effects, can only help wildlife management tactics, whether they are for endangered or nuisance species. Using the wrong type of vocalization for the wrong purpose can have unwanted effects on the species or on the property under protection (Bishop et al. 2003). Empirically testing the effects of playbacks of vocalizations on conspecifics should be the first step before the use of a bio-acoustic deterrent.

In addition, recent research into the cognitive and social coordination abilities of animals, especially birds, demonstrates that there is much yet to be learned about vertebrate social systems and how they contribute to individual survival (Gajdon et al. 2004, Diamond et al. 2006, Heinrich and Bugnyar 2005, Seed et al. 2008). As many raptor species are not thought of as social (Newton 1979), the few exceptions are worth detailed investigation to determine how cooperative behavior may have emerged independently within a group. Besides Greenland and mainland Antarctica, southern South America is the only major world region that supports no corvid species (Goodwin 1986). Thus it is possible that the Falkland Islands at one time presented an unoccupied corvid-like niche to an already broadly adaptive raptor species. The Striated Caracara exhibits many behavioral and even superficial qualities shared by Common Ravens or European Rooks, filling the niche of the opportunistic, social scavenger and leaving the solitary, avian ambush predator niche to the other endemics: the Red-backed Hawk and Peregrine Falcon. Investigations into the fossil record of the caracara and approximating the date of its arrival in the Falklands would be helpful in illuminating the early stages of the development of this behavior.

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Fig. 1.1 **Saunders Island settlement. Yellow star indicates location of the pig pen, black circle indicates scientist living quarters and site of 18 of 23 carcass trials. Image date: 26 December 2011. Approx. 0.7 km^2 area (Google Earth).**

Fig. 1.2 The pig pen. Five Striated Caracaras (3 juveniles, 1 subadult, 1 adult) perched on the railing, with two pigs inside the pen. Saunders Island, Falkland Islands, 2014 (A. Autilio).

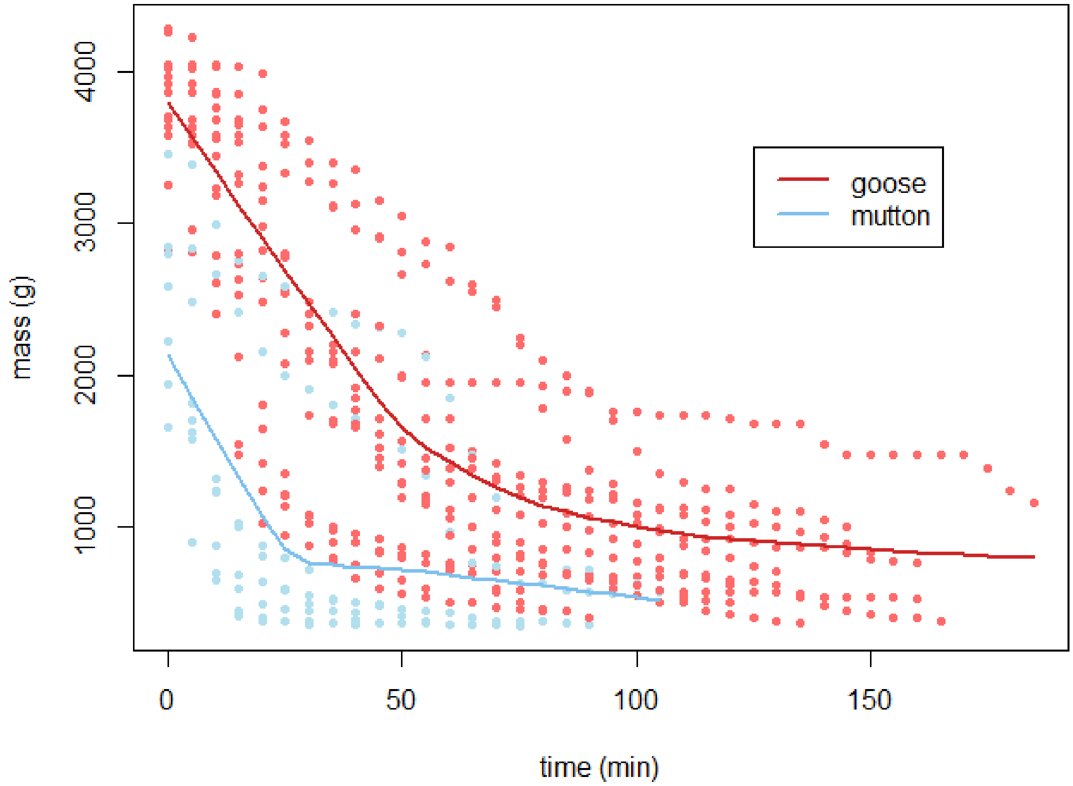

Fig. 1.3 **Carcass mass versus time for both mutton (n=8) and goose carcasses (n=15). Lines are lowess smoothing lines: values determined by linear least squares regression. Simple linear depletion rate averaged 29.0 g/min for goose carcasses, and 37.5 g/min for mutton carcasses.**

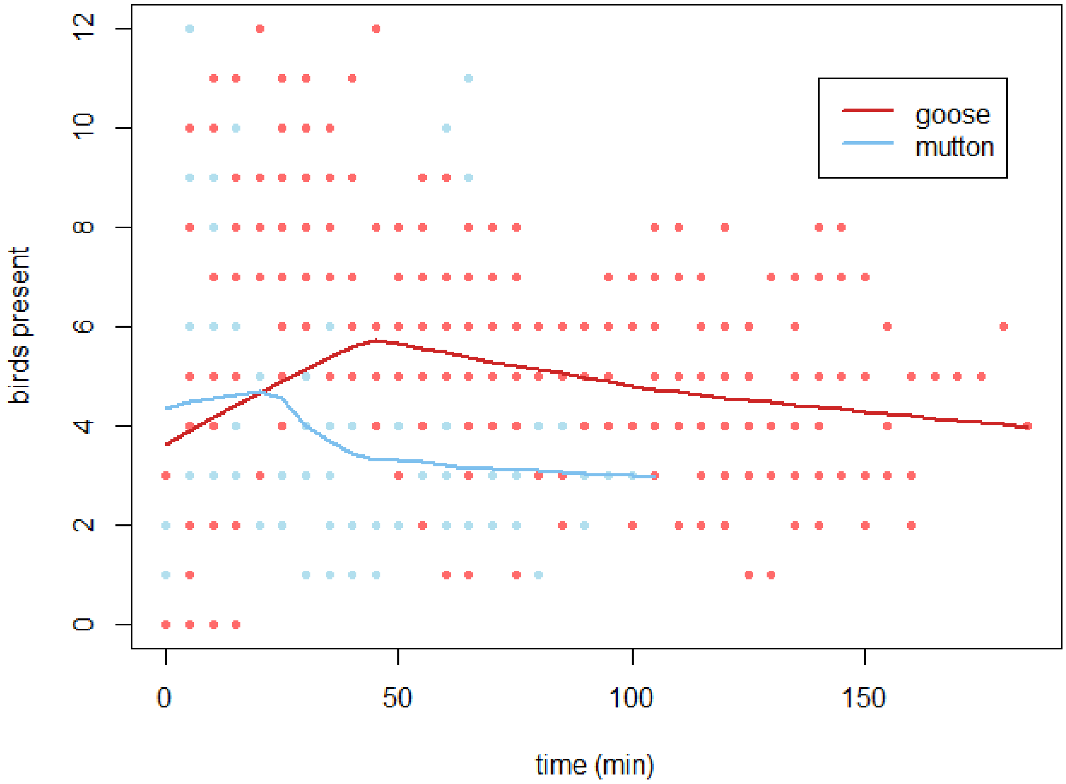

Fig. 1.4 Birds present and actively eating goose and mutton carcasses over time. Lines are lowess smoothing lines: values determined by linear least squares regression.

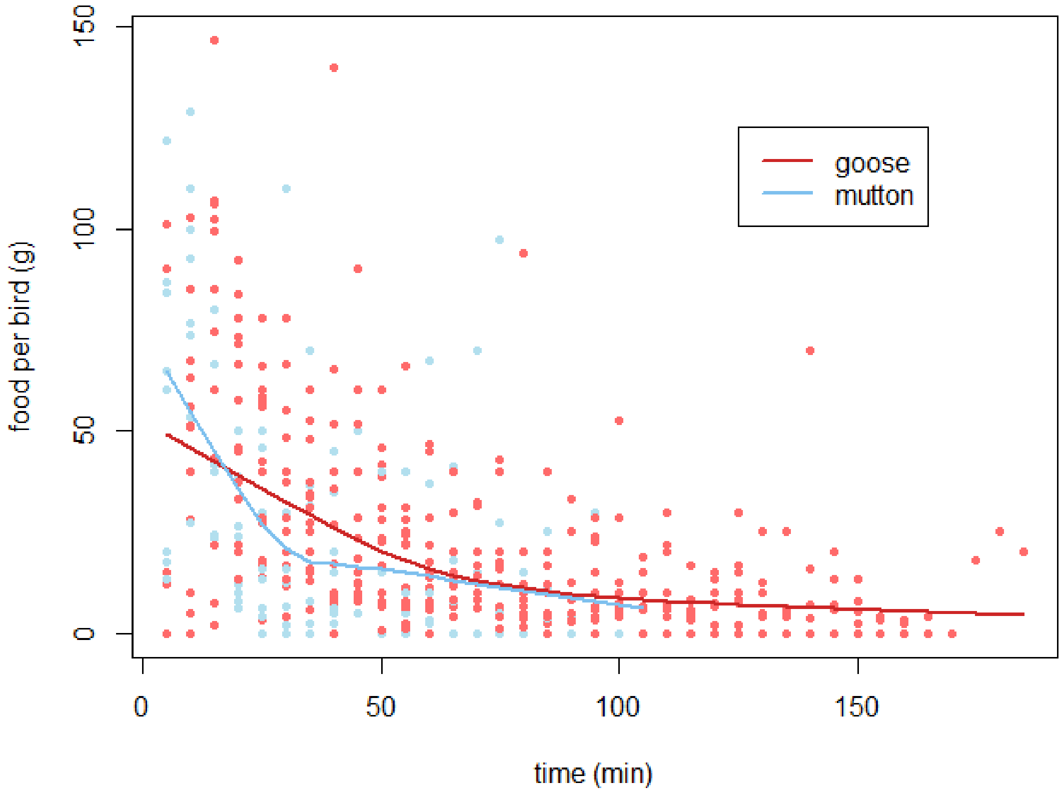

Fig. 1.5 **Food per bird over time for both goose and mutton carcasses. Lines are lowess smoothing lines: values determined by linear least squares regression.**

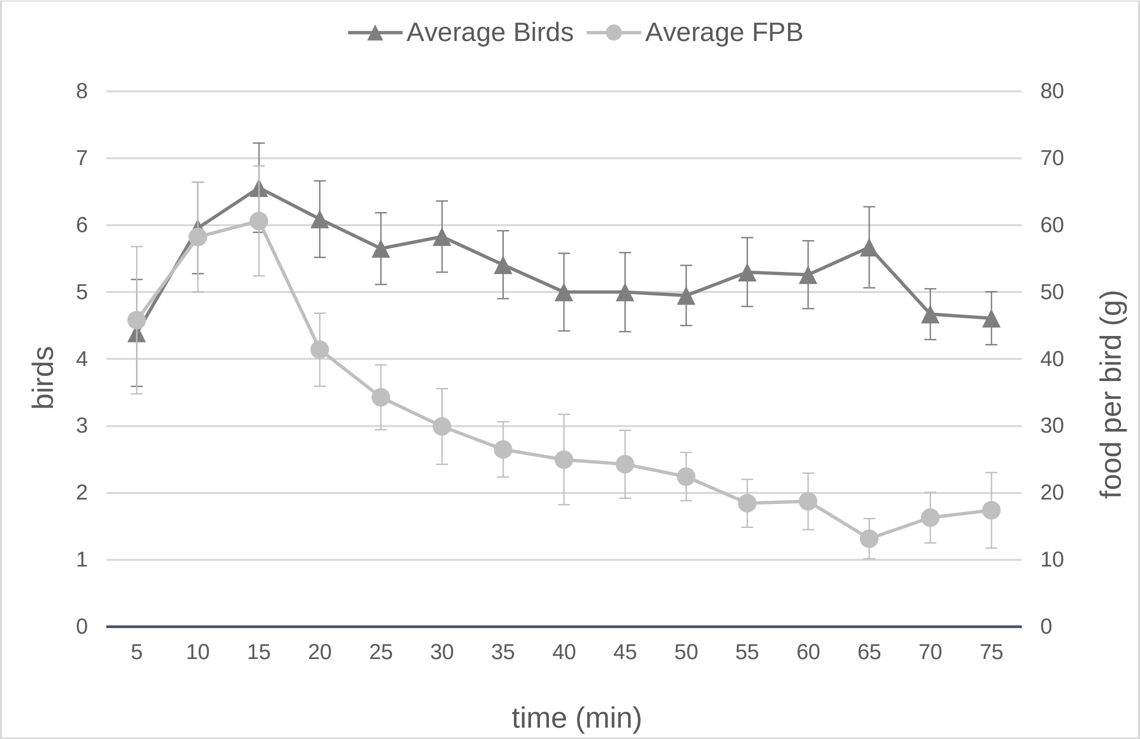

Fig. 1.6 **Comparing FPB and total birds averaged for each carcass (n = 23) at each time interval. Within the first 30 minutes of carcass availability, the number of birds and the food obtained by each increase and decrease together, but as the carcass becomes depleted, the trend becomes mirrored.**

Figure 2.1 Juvenile “hunched” vocalization posture (a) and adult pair display posture (b). Saunders Island, Falkland Islands, 2015 (A. Autilio).

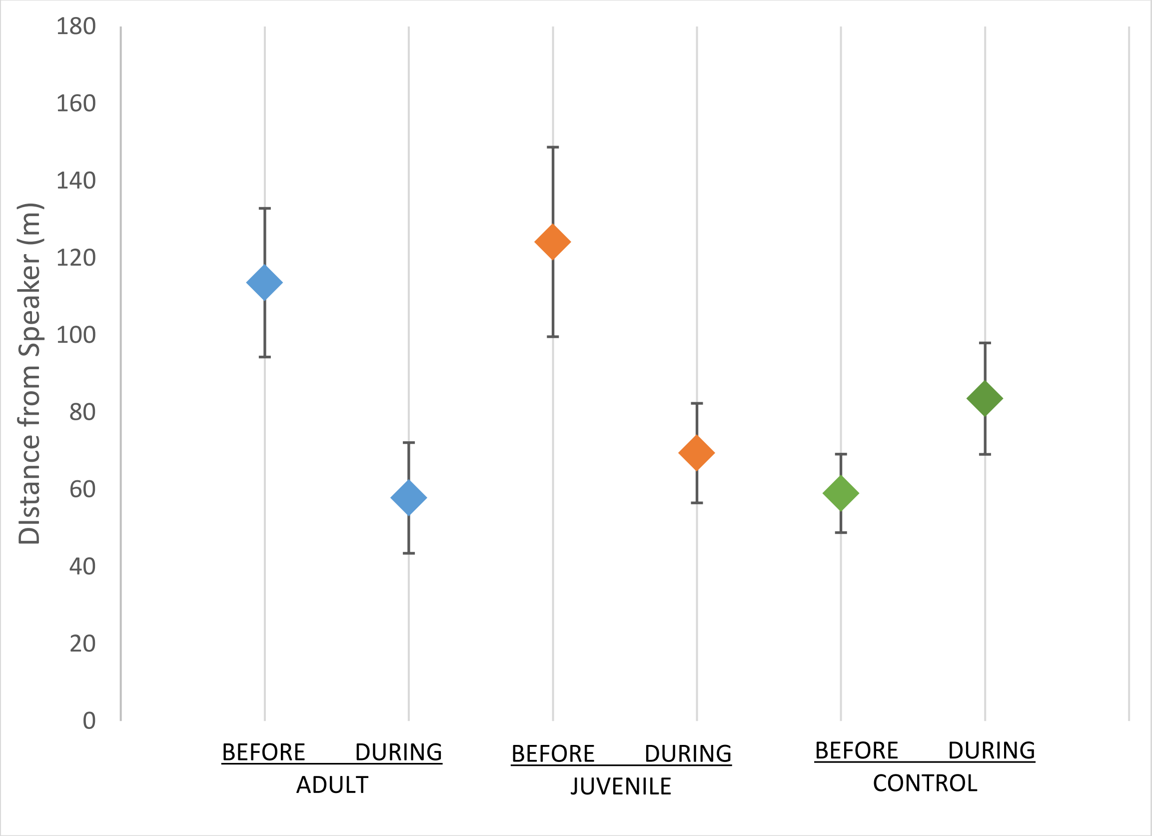

Figure 2.2 Mean distances of birds to speaker before and during each experimental trial. Error bars show standard error of the mean.

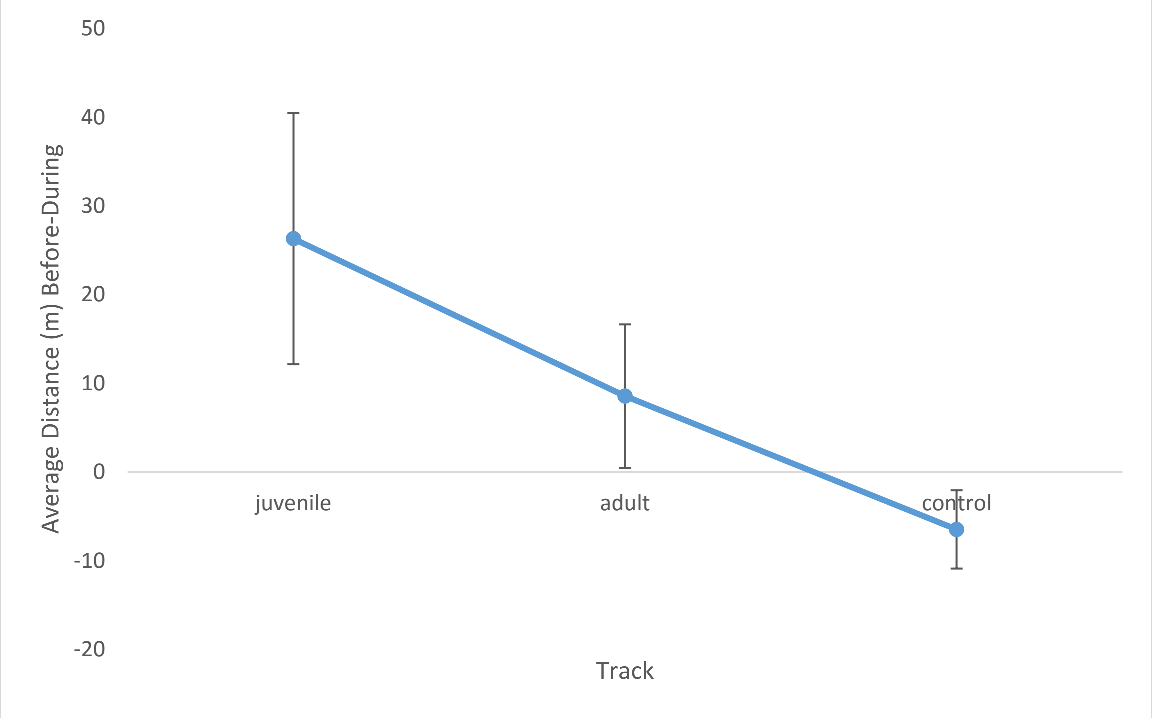

Figure 2.3 Difference in mean distance individuals approached the speaker. Positive values indicate birds moved closer to the speaker after the recording began. Error bars indicate the standard error of the mean. Shows a significant difference between distance approached between juvenile, adult, and control trials (Kruskal-Wallis $X^2 = 7.2507$, $p= 0.02664$).

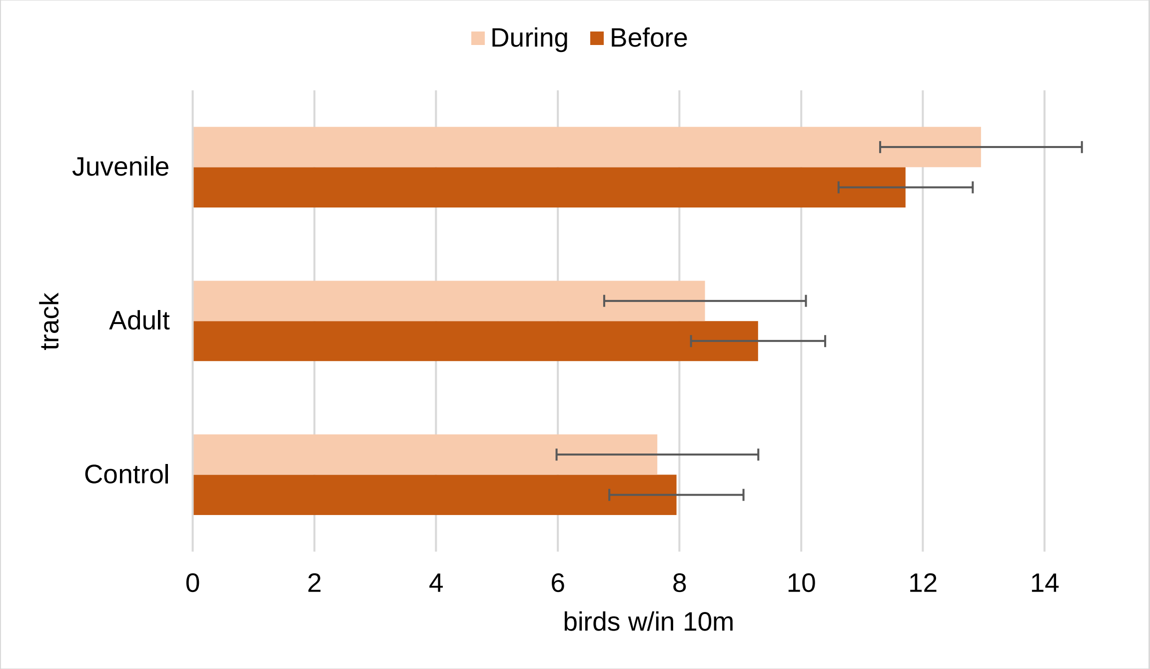

Figure 2.4 Mean number of birds within 300m of speaker before and during each experimental trial. Error bars show standard error of the mean.

Table 1.I Comparison of means of observations in both carcass types (means reported with standard errors)

	Goose (n=15)	Mutton (n=8)
Initial mass (g)	3820 (±100)	2540 (±200)
Discovery time[a] *(min)*	3.4 (±1.6)	0.8 (±0.3)
Birds eating[b]	5.1 (±0.1)	4.2 (±0.2)
% eaten	82.4 (±2.2)	83.2 (±1.0)
Depletion time (min)	125 (±10)	65 (±10)
Depletion rate (g/min)	29.0 (±3.3)	37.5 (±6.3)
FPB[c] *(g/bird)*	21.2 (±1.3)	28.9 (±2.5)

[a] Minutes until first individual arrived within 5m of carcass.

[b] Number of individuals actively eating during each 5 minute interval.

[c] Food per bird. Estimated mass of carcass consumed per individual over a 5 minute interval.

Table 1.II Summary of AIC$_c$ output on candidate model set explaining FPB ("time" = minutes from start, "birds" = total birds eating, "ad" = proportion of adults, "juv" = proportion of juveniles, "mass" = carcass (g), "type" = mutton or goose.

Model	*K*	*AICc*	*ΔAICc*	*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

Table 1.III Summary of top 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 per bird at all carcasses. Adjusted R-squared = 0.2972, residual standard error = 22.24

Variables	*Model Estimate*	*Standard Error*	*t-value*	*p-value*
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

Table 2.I Model output for log-linked model of average distance of birds to speaker during treatments. SITE = distance from settlement, TRACK = treatment type.

	Model Estimates		
Variable	**β**	**SE**	**p**
SITE	-1.527	0.032	<0.0001
TRACK - CONTROL	0.553	0.027	<0.0001
TRACK - JUVENILE	0.159	0.029	<0.0001