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SOCIAL HIERARCHY OF SCAVENGING RAPTORS ON THE FALKLAND ISLANDS, MALVINAS

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ABSTRACT.—On the Falkland Islands (Malvinas), raptors historically were perceived as a threat to livestock, and consequently were widely persecuted through the mid-twentieth century. Conservation measures now minimize persecution and have facilitated increases in raptor populations, but the ecology of raptors on the Falkland Islands (Malvinas) remains poorly understood. We investigated social hierarchies within an assemblage of non-migratory raptorial scavengers: Variable Hawk (*Buteo polyosoma*), Striated Caracara (*Phalacrocorax australis*), Southern Caracara (*Caracara plancus*), and Turkey Vulture (*Cathartes aura jota*). During thirty observation sessions of 30 min each, we recorded 1386 aggressive interactions involving one or more of these species. We found that Variable Hawks were aggressors in 98% (95% CI = 96–100%) of interactions with Striated Caracaras, 82% (69–95%) of interactions with Turkey Vultures, and 80% (72–88%) of interactions with Southern Caracaras. Southern Caracaras were aggressors in 100% of interactions with Striated Caracaras, and 90% (80–100%) of interactions with Turkey Vultures. Turkey Vultures were aggressors in 71% (61–82%) of interactions with Striated Caracaras. Within species, we found adult Southern Caracaras were aggressors in 78% (72–84%) of interactions with conspecific juveniles and 76% (68–85%) of interactions with conspecific subadults. Adult Striated Caracaras were aggressors in 100% of interactions with conspecific juveniles and 97% (91–100%) of interactions with conspecific subadults. Predicted patterns of size-based dominance typical of complex African and South American avian scavenger assemblages were not observed in the relatively simple assemblage of the Falkland Islands (Malvinas), but we did observe single-species groups of up to 83 Southern Caracaras and 42 Striated Caracaras.

KEY WORDS: *Southern Caracara*; *Caracara plancus*; *Striated Caracara*; *Phalacrocorax australis*; *Turkey Vulture*; *Cathartes aura*; *Variable Hawk*; *Buteo polyosoma*; *behavior*; *scavenger*; *social hierarchy*.

JERARQUÍA SOCIAL DE RAPACES CARROÑERAS EN LAS ISLAS MALVINAS

RESUMEN.—En las Islas Malvinas, las rapaces han sido percibidas históricamente como una amenaza para el ganado y consecuentemente han sido ampliamente perseguidas durante la mitad del siglo veinte. Las medidas de conservación han minimizado la persecución permitiendo el aumento de las poblaciones de rapaces, pero su ecología en las Islas Malvinas permanece poco conocida. Investigamos las jerarquías sociales dentro de un ensamble de rapaces carroñeras no migratorias: *Buteo polyosoma*, *Phalacrocorax australis*, *Caracara plancus* y *Cathartes aura jota*. Durante treinta secciones de observación de 30 min cada una, registramos 1386 interacciones agresivas involucrando una o más de estas especies. Encontramos que los individuos de *B. polyosoma* fueron agresores en 98% (95% IC = 96–100%) de las interacciones con *P. australis*, 82% (69–95%) de las interacciones con *C. aura* y 80% (72–88%) de las interacciones con *C. plancus*. Los individuos de *C. plancus* fueron agresores en 100% de las interacciones con *P. australis* y 90% (80–100%) de las interacciones con *C. aura*. Los individuos de *C. aura* fueron agresores en 71% (61–82%) de las interacciones con *P. australis*. En cada especie, encontramos que los adultos de *C. plancus* fueron agresores en 78% (72–84%) de las interacciones con los juveniles coespecíficos y 76% (68–85%) de las interacciones con los subadultos coespecíficos. Los adultos de *P. australis* fueron agresores en 100% de las interacciones con los juveniles coespecíficos y 97% (91–100%) de las interacciones con los subadultos coespecíficos. Los patrones predichos de dominancia basados en el tamaño, típicos de los ensambles complejos de aves carroñeras de África y Sud América no fueron observados en los ensambles relativamente simples de las Islas Malvinas, pero observamos grupos de una sola especie de hasta 83 individuos de *C. plancus* y 42 individuos de *P. australis*.

[Traducción del equipo editorial]

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On the Falkland Islands (Malvinas), official bounties were offered for the bills of raptors from 1909 (Woods and Woods 1997) until 1946 as part of a predator eradication program (Meiburg 2006). Private bounties and persecution also existed before and continued after that period (Strange 1996) until bounties were outlawed in 1964 (Falkland Islands Government 1999). Facultative and obligate raptorial avian scavengers now occur widely throughout the archipelago (Woods and Woods 1997, Woods 2007) including four large, nonmigratory species (Ferguson-Lees and Christie 2001, Woods and Woods 2006) regularly found foraging together at carcasses (Breen and Bildstein 2008). From smallest to largest by mass (Table 1), these are Variable Hawk (*Buteo polyosoma*), Striated Caracara (*Phalacrocorax australis*), Southern Caracara (*Caracara plancus*), and Turkey Vulture (*Cathartes aura jota*).

Typically, all individuals do not pay identical costs when foraging socially (Lemon 1991, Newton 1998). Rather, competition costs are borne disproportionately by the lowest ranking members in the social hierarchy (Newton 1979). Though competition for resources is one of the most common costs of social foraging (Krause and Ruxton 2002), competitive interactions and social hierarchies have not been investigated for raptorial scavengers on the Falkland Islands (Malvinas), and little is known of their social ecology (Catry et al. 2008).

Social hierarchies among avian scavengers are most often determined by size and age, such that between species larger species are dominant over smaller ones, and within species older individuals are dominant over younger ones (Newton 1979, Wallace and Temple 1987, Krause and Ruxton 2002). However, Wallace and Temple (1987) found that Southern Caracaras in Peru were dominant over larger Turkey Vultures and Black Vultures, and Travaini et al. (1998) found Southern Caracaras were equally ranked with Black Vultures in Patagonia. We hypothesized that hierarchies within the avian scavenger assemblage on the archipelago would parallel patterns identified in similar, but more complex, assemblages of South America. Consequently, we predicted that Southern Caracaras would be dominant over Turkey Vultures, but that the remainder of the avian scavenger hierarchy would be dictated by the size of each species. Wallace and Temple (1987) also found that adult Southern Caracaras outranked juveniles, and we hypothesized that this would occur for both caracara species on the Falkland Islands (Malvinas).

STUDY AREA AND METHODS

The Falkland Islands (Malvinas) lie approximately 500 km east of southern Argentina in the Atlantic Ocean from 51°S to 53°S, and from 57°W to 61°W. The land area of the archipelago totals approximately 12 170 km² (FAO-UN 2011), and comprises two large islands, East Falkland and West Falkland, and over 700 smaller islands (Woods 2001). Maximum elevation is 705 m above sea level, and the climate is dominated by strong winds (annual mean of 27 km per hr) and cool temperatures (annual mean of 6°C; Woods and Woods 2006). The archipelago supports approximately 3000 permanent residents (FAO-UN 2011) and a military garrison (Falkland Islands Government 2011) of about 2000 (Woods and Woods 2006). Approximately 92% of the archipelago is managed as permanent pasturage (FAO-UN 2011) supporting an estimated 600 000 sheep (*Ovis aries*) and 5000 cattle (*Bos taurus*; Falklands Island Government 2011). Natural vegetation is dominated by grasses and shrubs <2 m tall, and the islands lack any native trees (Hall et al. 2002, Woods and Woods 2006).

We collected observations at six sites on West Falkland Island and at one site on East Falkland Island between 24 July and 13 August 2010. We sought groups of avian scavengers at each site and conducted a 30-min group sample (Martin and Bateson 2007) each time we observed a group. We separated samples by a least 1 hr or 1 km to ensure that sampling incorporated as many individuals and group compositions as possible. During group samples, we recorded the aggressor and receiver of all aggressive interactions by all group members (Wallace and Temple 1987, Kirk and Houston 1995, Travaini et al. 1998). Most of the carcasses where we observed interactions were those of Upland Goose (*Chloephaga picta leucoptera*) harvested by landowners as food for domestic animals or as a wildlife control strategy to minimize competition between geese and sheep.

We distinguished between low-intensity and high-intensity aggressive interactions. We defined high-intensity interactions as including physical contact, an airborne or foot chase of >1 m, kleptoparasitism, or a supplant wherein a stationary bird was displaced by a group member that occupied the displacement point immediately thereafter. In these cases the intent of the aggressor and the intended recipient were clear. We defined low-intensity interactions as those aggressions where we were not always sure of the intent of the potential aggressor or

Table 1. Sizes and conservation status of scavenging raptors on the Falkland Islands (Malvinas).

SPECIES ^a	MASS (g)	LENGTH ^b (cm)	WINGSPAN ^b (cm)	STATUS (NUMBER OF PAIRS)
VAHA	950 ^c (<i>n</i> = 1)	46–56	110–120	Common; 500–1000 ^b
STCA	1500 ^d (<i>n</i> = 10)	58–63	about 12	Near threatened; about 500 ^b
SOCA	1600 ^d (<i>n</i> = 7)	49–59	120–132	Common; 400–800 ^b
TUVU	2100 ^d (<i>n</i> = 3)	66–71	157–170	Abundant; 4170–6050 ^c

^a SOCA = Southern Caracara, VAHA = Variable Hawk, STCA = Striated Caracara, TUVU = Turkey Vulture.

^b Woods and Woods 2006.

^c Ferguson-Lees and Christie 2001.

^d S.G. Cockwell and C. Dockrill, unpubl. data.

^e Breen and Bildstein 2008.

the identity of an individual intended recipient. In these cases vocalizations, head-back displays, (Strange 1996) and mantling might be directed at more than one individual. Similarly, “flushes” wherein a stationary bird moved away from an approaching bird, but the approaching bird did not occupy the displacement point immediately thereafter, may not have indicated true aggression.

We aged Striated Caracaras and Southern Caracaras by plumage. Juvenile Striated Caracaras have brown spots on the nape and shoulders, subadult birds have brown streaks, and adults have white streaks (Strange 1996). Age-related differences in Southern Caracaras have not been precisely described. However, the plumage of Southern Caracaras closely resembles the plumage of the congeneric Crested Caracaras (*Caracara cheriway*; Ferguson-Lees and Christie 2001) so we aged Southern Caracaras based on existing knowledge of Crested Caracaras. Juvenile Crested Caracaras have streaked breasts, subadults have breasts with a mix of streaks and bars, and adults have barred breasts (Wheeler and Clark 1995). We observed too few interactions involving Variable Hawks and Turkey Vultures to allow intraspecific analysis, so we do not report ages for these species.

For analysis, we compared all aggressions (including both low- and high-intensity interactions), and we compared high-intensity aggressions only. Wallace and Temple (1987) and Travaini et al. (1998) used proportions of interactions won by various species and ages to identify intra- and inter-specific hierarchies. We used a similar approach by identifying the 95% confidence interval for the proportion of interactions won by a certain species or age class. When a confidence interval was entirely above or below 50%, then we considered the species or age class dominant or subordinate, respectively. When a

95% confidence interval overlapped 50%, we concluded that we did not have evidence to support the hypothesis that a hierarchical relationship existed.

RESULTS

During thirty observation sessions of 30 min each, we observed 1386 aggressive interactions, including 713 high-intensity interactions. We observed single-species groups containing up to 83 Southern Caracaras, and 42 Striated Caracaras. We also observed mixed species groups containing up to 8 Turkey Vultures and 4 Variable Hawks. Using all interactions between species, we found that Variable Hawks were dominant over Southern Caracaras, Striated Caracaras, and Turkey Vultures (Table 2). Southern Caracaras were dominant over Turkey Vultures and Striated Caracaras, and Turkey Vultures were dominant over Striated Caracaras only. Each of these relationships was consistent when we limited our evaluation to high-intensity interactions, except that Turkey Vultures were equivalent to Striated Caracaras when only high-intensity interactions were considered. These relationships indicated the following hierarchy: Variable Hawk > Southern Caracara > Turkey Vulture > Striated Caracara, where “>” indicates that the preceding species is dominant over all subsequent species.

Within species, we found that adult Striated Caracaras were dominant over subadult and juvenile Striated Caracaras (Table 3), but we found no evidence of hierarchy between subadult and juvenile Striated Caracaras. These relationships were consistent regardless of whether we considered all interactions or high-intensity interactions only. We found the same pattern of intraspecific hierarchy for Southern Caracaras (Table 4).

We also recorded 94 instances of Striated Caracaras departing carrion when approached by a domes-

Table 2. Outcomes of aggressive interactions between species of avian scavengers on the Falkland Islands (Malvinas). Data collected from 24 July through 13 August 2010.

SPECIES ^a		ALL AGGRESSIONS ^b			HIGH-INTENSITY AGGRESSIONS ^c		
AGGRESSOR	RECEIVER	% WON	95% C.I.	<i>n</i>	% WON	95% C.I.	<i>n</i>
VAHA	SOCA	80.0	71.7–88.3	72	100.0	N/A	51
VAHA	TUVU	81.8	68.7–95.0	33	92.9	83.3–100.0	28
VAHA	STCA	98.0	95.8–100.0	151	78.6	57.1–100.0	14
SOCA	TUVU	90.3	79.9–100.0	31	100.0	N/A	11
SOCA	STCA	100.0	N/A	8	100.0	N/A	8
TUVU	STCA	71.2	60.9–81.6	73	63.2	47.8–78.5	38

^a SOCA = Southern Caracara, VAHA = Variable Hawk, STCA = Striated Caracara, TUVU = Turkey Vulture.

^b Aggression including vocal displays, visual displays, physical contact, and supplanting.

^c Aggressions including physical contact or supplanting only.

tic cat (*Felis catus*), and 21 instances of Striated Caracaras departing carrion when approached by a domestic pig (*Sus scrofa domesticus*). No other avian species were present during these interactions, and we did not observe any aggression directed at either cats or pigs by Striated Caracaras.

DISCUSSION

On the basis of body size, we predicted that Variable Hawks, the smallest scavenging raptor (950 g) on the Falkland Islands (Malvinas) would be subordinate to all other scavenging raptors on the archipelago. Our prediction was supported by reports of intra-guild aggression on South America directed toward Variable Hawks (Jiménez and Jaksic 1989) by Black-chested Buzzard-Eagles (*Geranoaetus melanoleucus*; 2300–3033 g), Harris's Hawks (*Parabuteo unicinctus*; 700 g), a Chimango Caracara (*Milvago chimango*; 295–482 g), and an American Kestrel (*Falco sparverius*; 130–163 g; species' masses from Jaksic et al. 2002). Jaksic et al. (2002) also reported a Variable Hawk chased by a Black-chested Buzzard-Eagle, and Orellana and Rojas (2005) described an

adult Harris's Hawk pursuing a juvenile Variable Hawk in flight. Jiménez and Jaksic (1991) found that aggressive interactions occupied <2% of Variable Hawk's time in central Chile. Given the Variable Hawk's relatively subordinate role in South American raptor assemblages, its dominant role on the Falkland Islands (Malvinas) is surprising.

Southern Caracaras (1600 g) were subordinate to Variable Hawks, but dominant over Turkey Vultures (2100 g). This is consistent with findings by Wallace and Temple (1987) wherein Southern Caracaras were dominant over Turkey Vultures and Black Vultures (*Coragyps atratus*; 1180–1940 g, Ferguson-Lees and Christie 2001) in Northern Peru. Dwyer (2010) also found that closely related Crested Caracaras were dominant over Turkey Vultures and Black Vultures in Florida, U.S.A. In Peru, Southern Caracaras were subordinate only to Andean Condors (*Vultur gryphus*; 9500–12 500 g) and King Vultures (*Sarcophagus papa*; 3000–3700 g), and in Florida, Crested Caracaras were subordinate only to Bald Eagles (*Haliaeetus leucocephalus*; 3680–6410 g, Buehler 2000). Thus, it is also surprising that a species which is

Table 3. Outcomes of aggressive interactions among Striated Caracaras on the Falkland Islands (Malvinas). Data collected from 24 July through 13 August 2010.

AGE ^a		ALL AGGRESSIONS ^b			HIGH-INTENSITY AGGRESSIONS ^c		
AGGRESSOR	RECEIVER	% WON	95% C.I.	<i>n</i>	% WON	95% C.I.	<i>n</i>
ADUL	SUBA	76.5	68.1–84.9	98	74.5	62.6–86.5	51
ADUL	JUVE	78.3	72.3–84.4	180	66.7	57.4–76.0	99
SUBA	JUVE	44.3	34.9–53.8	106	40.8	29.7–51.8	76

^a ADUL = Adult, SUBA = Subadult, JUVE = Juvenile.

^b Aggression including vocal displays, visual displays, physical contact, and supplanting.

^c Aggressions including physical contact or supplanting only.

Table 4. Outcomes of aggressive interactions among Southern Caracaras on the Falkland Islands (Malvinas). Data collected from 24 July through 13 August 2010.

AGE ^a		ALL AGGRESSIONS ^b			HIGH-INTENSITY AGGRESSIONS ^c		
AGGRESSOR	RECEIVER	% WON	95% C.I.	<i>n</i>	% WON	95% C.I.	<i>n</i>
ADUL	SUBA	97.1	91.4–100.0	34	100.0	N/A	32
ADUL	JUVE	100.0	N/A	22	100.0	N/A	18
SUBA	JUVE	33.3	0.0–86.7	3	50.0	0.0–100.0	2

^a ADUL = Adult, SUBA = Subadult, JUVE = Juvenile.

^b Aggression including vocal displays, visual displays, and physical contact.

^c Aggressions including physical contact or supplanting only.

usually dominant over all but its largest competitors in South America and North America is subordinate to the Variable Hawk, a species only two-thirds the Southern Caracara’s size, on the Falkland Islands (Malvinas).

On the Falkland Islands (Malvinas), Striated Caracaras feed on young penguins, geese, albatross, and their eggs. Groups of Striated Caracaras attack apparently healthy native species much larger than themselves, and are reported to attack lambs and injured or immobilized sheep (Ferguson-Lees and Christie 2001, Woods and Woods 2006, Liljeström et al. 2008). Given their aggressiveness in pursuing live prey, it is also surprising to find Striated Caracaras at the bottom of the scavenging raptor hierarchy. Only the relatively subordinate role of Turkey Vultures on the Falkland Islands (Malvinas) was consistent with their typical status in hierarchies elsewhere in their range.

The unexpected hierarchy of avian scavengers on the Falkland Islands (Malvinas) requires explanation. We offer three competing hypotheses. First, the limited nature of our study may have captured an unrepresentative sample of interactions. We report data from unmarked individuals during only three weeks of observations collected at only six sites during a nonbreeding season. If inter- or intraspecific interactions differ with seasonal differences in resources, breeding status, or other factors, or if individual variation occurs, our study would not indicate the importance of these factors. Dockrill and Cockwell (unpubl. data) found aluminum leg bands, colored plastic leg bands, radio-tags, and satellite tracking devices each were effective identification tools for both Southern Caracaras and Striated Caracaras. Given the surprising hierarchy reported here, future research should use these techniques to identify whether dominance is consistent

throughout the year, and whether specific individuals may be dominant within groups.

Second, differences in prey abundance or availability on the Falkland Islands (Malvinas) relative to the South American continent may drive competitive interactions between avian scavengers on the archipelago in unexpected ways. Differences between South America and the Falkland Islands (Malvinas) could be exaggerated in this study focusing on areas where human residents routinely disposed of carrion, and which local scavengers likely routinely visited to evaluate resource availability. Our use of established foraging areas precluded collection of unbiased information on the arrival order of species as a carcass is discovered. Because different species use different hunting strategies, which can influence the arrival timing of species at a carcass, which can in turn influence competition at a carcass, future research should investigate the arrival of avian scavengers on the Falkland Islands (Malvinas) at sites where carcasses might be less predictable.

Third, differences in raptor diversity between the Falkland Islands (Malvinas) and South America may influence the relationships reported here. There is relatively little raptor diversity on the Falkland Islands (Malvinas). Peregrine Falcons (*Falco peregrinus*) are the only other diurnal raptor on the archipelago, but Peregrine Falcons were not present during this nonbreeding season study, and only rarely consume carrion (Holland 1989, Ferguson-Lees and Christie 2001). In contrast, up to 60 diurnal raptors including condors, vultures, kites, harrisers, hawks, eagles, caracaras, and falcons overlap at least portions of the Variable Hawk’s range in South America (Ferguson-Lees and Christie 2001), and the ranges of over 90 diurnal raptor species overlap the combined ranges of Southern Caracara and Crested Caracara in South and North America.

Though habitat use minimizes the likelihood of interactions with many of these species, the avian scavenger assemblages are nevertheless far more complex on the American continents than they are on the Falkland Islands (Malvinas).

Intraspecific hierarchies were less surprising. Regardless of whether we considered all aggressive interactions, or high-intensity interactions only, we found consistent evidence that adult Southern Caracaras and adult Striated Caracaras were dominant over conspecific subadults and juveniles. These findings reflect similar patterns reported for avian scavenger assemblages in Peru (Wallace and Temple 1987), Florida (Dwyer 2010), and Baja California (Rodríguez-Estrella and Rivera-Rodríguez 1992). In many species, young birds are less efficient foragers than older birds (Burger 1988, Marchetti and Price 1989, Wunderle 1991). In Florida, juvenile and subadult Crested Caracaras apparently gain social learning benefits that offset competition costs (Dwyer 2010), and a similar mechanism may operate in the Falkland Islands (Malvinas).

We recorded the outcome of aggressive interactions in terms of aggressors and receivers during interactions. We did not record the subsequent behavior of participants, but we can report anecdotally that receivers of aggression usually retreated less than a meter from the aggressor and then resumed pre-aggression activity without receiving additional aggression. Thus, a subordinate bird supplanted from carrion often simply resumed feeding at the opposite side of the carrion from where the aggression occurred. By contrast, when an aggressive individual was rebutted with aggression, the aggression typically escalated until the losing bird was driven from view during an aerial chase. Thus, there appeared to be a relatively low cost to accepting aggression and a potentially high cost to retaliating. Turkey Vultures in particular appeared to ignore aggression by continuing to feed alongside their much smaller aggressors.

We observed relatively large groups of Southern Caracaras and Striated Caracaras, and groups of up to 60 Turkey Vultures (Breen and Bildstein 2008) have been reported on the Falkland Islands (Malvinas). Though legal protection now exists for avian scavengers on the Falkland Islands (Malvinas), and our observations indicate that healthy domestic animals can supplant avian scavengers, concern persists among human residents that single-species and mixed species groups of Southern Caracaras, Striated Caracaras, and Turkey Vultures may pose

a threat to lambs and to injured or immobilized sheep (Woods and Woods 2006, Breen and Bildstein 2008). Future research should focus on using scientific protocols to investigate damage to livestock, if it occurs.

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