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CORRELATION OF CERE COLOR WITH INTRA- AND INTERSPECIFIC AGONISTIC INTERACTIONS OF CRESTED CARACARAS

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ABSTRACT.—Bright coloration in birds is an important indicator of individual quality often used in social displays. Structural, carotenoid-, and melanin-based colors are long-lasting, widespread, and widely studied. Hemoglobin-based colors are ephemeral, rare, and less studied. Hemoglobin-based displays occur when an individual facultatively enhances or restricts blood flow through caruncles, combs, wattles, or other highly vascularized un-feathered skin patches. In Crested Caracaras (*Caracara cheriway*; hereafter ''caracara'') highly vascularized ceres facultatively undergo immediately reversible hemoglobin-based color changes, hypothesized to correlate with status during contests. I predicted aggressors in contests would consistently display hemoglobin-deprived ceres (hereafter ''light''), and receivers would display hemoglobin-enhanced ceres (hereafter ''dark''), or vice versa. To test this hypothesis, I conducted 149 30-min group observations during which I recorded outcomes of all observed intra- and interspecific agonistic interactions involving caracaras in groups including up to 46 caracaras ($\bar{x}$ = 13.4, SD = 6.9). I recorded 2586 agonistic interactions in which I could identify cere colors and ages of both caracaras involved in an intraspecific interaction (n = 1160), or of one caracara involved in an interspecific interaction (n = 1426). Cere colors of caracaras were consistently light when acting as aggressors in intra- and interspecific agonistic interactions, and dark when acting as receivers. Within age classes, caracaras displaying light-colored ceres were consistently aggressors toward caracaras displaying dark ceres, and between age classes, adults with light-colored ceres were aggressors toward younger birds with dark ceres. Caracaras displaying light-colored ceres were aggressors toward Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) and caracaras with dark ceres were receivers of aggression from these species. Regardless of the cere color, caracaras were subordinate to much larger Bald Eagles (*Haliaeetus leucocephalus*) and dominant over much smaller American Crows (*Corvus brachyrhynchos*). My observations support the hypothesis that cere color is correlated with agonistic behaviors and support the signaling hypothesis by correlating specific cere colors displayed with individual roles in intra- and interspecific interactions.

KEY WORDS: *Crested Caracara*; Caracara cheriway; *cere*; *facial flushing*; *Florida*; *nonbreeding*; *social hierarchy*.

CORRELACIÓN DEL COLOR DE LA CERA CON INTERACCIONES AGONÍSTICAS INTRA E INTERESPECÍFICAS DE *CARACARA CHERIWAY*

RESUMEN.—En las aves, la coloración brillante es un indicador importante de calidad individual que se usa a menudo en los despliegues sociales. Los colores estructurales y basados en carotenoides y melanina han sido estudiados desde hace tiempo y de forma amplia y generalizada. Los colores basados en la hemoglobina son efímeros, raros y menos estudiados. Los despliegues basados en la hemoglobina ocurren cuando un individuo aumenta o restringe facultativamente el flujo sanguíneo a través de las carúnculas, crestas u otros parches de piel sin plumas altamente vascularizados. En *Caracara cheriway*, las ceras altamente vascularizadas experimentan de forma facultativa cambios de color inmediatamente reversibles basados en la hemoglobina, los cuales se piensa que están correlacionados con el estatus durante las competencias. Predije que en una competencia, los individuos agresores desplegarían consistentemente ceras carentes de hemoglobina (de aquí en más ''claras'') y que los individuos que reciben la agresión desplegarían ceras realzadas por la hemoglobina (de aquí en más ''oscuras'') o viceversa. Para evaluar esta hipótesis, realicé 149 observaciones grupales de 20 minutos cada una durante las cuales registré los resultados de todas las interacciones agonísticas intra e inter-específicas observadas que involucraban a ejemplares de *C. cheriway* en grupos de hasta 46 individuos ($\bar{x}$ = 13.4, DE = 6.9). Registré 2586 interacciones agonísticas en las cuales pude identificar el color de la cera y las edades de ambos individuos involucrados en una interacción intra-

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específica (n = 1160), o de un individuo involucrado en una interacción inter-específica (n = 1426). Los colores de la cera de los individuos fueron consistentemente claros cuando actuaban como agresores en interacciones agonísticas intra e inter-específicas y oscuros cuando actuaban como receptores de la agresión. Dentro de las clases de edad, los individuos que desplegaban ceras claras fueron consistentemente agresivos con individuos que desplegaban ceras oscuras y, entre las clases de edad, los adultos con ceras claras fueron agresivos con aves más jóvenes de ceras oscuras. Los individuos de *C. cheriway* con ceras claras fueron agresivos con individuos de *Coragyps atratus* y *Cathartes aura* y los individuos de *C. cheriway* con ceras oscuras fueron receptores de agresiones de estas especies. Independientemente del color de la cera, los individuos de *C. cheriway* fueron subordinados por individuos más grandes de *Haliaeetus leucocephalus* y dominantes sobre individuos más pequeños de *Corvus brachyrhynchos*. Mis observaciones apoyan la hipótesis de que el color de la cera está correlacionado con comportamientos agonísticos y apoyan la hipótesis de señalización, correlacionando los despliegues de colores específicos de la cera con los roles individuales en interacciones intra e inter-específicas.

[Traducción del equipo editorial]

Bright coloration is an important avian characteristic indicative of individual quality and used in both intraspecific and interspecific signals. Typically, more brightly colored individuals have higher relative fitness than less brightly colored individuals of the same sex and species (Maynard-Smith and Harper 2004, Bradbury and Vehrencamp 2011). Bright coloration is an honest signal of individual quality because the structures, carotenoids, melanin, and hemoglobin required to produce bright colors reflect an individual's ability to secure resources and to maintain resources levels despite competing needs. Though bright coloration can be an effective signal, the accuracy of the signal has the potential to attenuate over time because, for example, carotenoid-based scales and melanin-based feathers can persist long after the conditions in which they were grown (Maynard-Smith and Harper 2004, Negro et al. 2006).

In contrast to structural, carotenoid-, and melanin-based colors, hemoglobin-based colors can facilitate reversible bright color changes within seconds, providing immediate signals via blood flow within the body. Hemoglobin-based displays occur when an individual facultatively enhances or restricts blood flow through highly vascularized caruncles, combs, wattles, or other highly vascularized unfeathered skin patches (Negro et al. 2006). Species that can rapidly change the color of bare skin tend to be large birds with dark plumage and, among raptors, typically occupy hot environments (Negro et al. 2006). These species can have high internal heat loads, and highly vascularized exposed skin may have evolved to facilitate thermoregulation by allowing warm blood to be circulated from the internal organs to the body's surface where heat can be dissipated (Negro et al. 2006). Observations of facial flushing during agonistic interactions suggest a signaling system may have been superimposed on this thermoregulatory process (Negro et al. 2006). For example, bare skin on the head of Lappet-faced Vultures (*Torgos tracheliotos*) is facultatively changed from pink to deep red and back again within seconds, and these changes correlate with the outcomes of intraspecific interactions (Bamford et al. 2010). Individuals displaying deep red skin consistently win intraspecific agonistic interactions with individuals displaying pink skin. As signals of dominance in feeding hierarchies, Andean Condors (*Vultur gryphus*) change the color of bare skin on the head from pale pink, yellow, or grey to deep yellow, orange, or red within a few seconds during contests at carcasses (Blanco et al. 2013). Also during contests at carcasses, Hooded Vultures (*Necrosyrtes monachus*) facultatively change the skin color of their mostly un-feathered heads from pink to purplish-red during intraspecific interactions (Negro et al. 2006).

Color variation has been recorded for the ceres of Crested Caracaras (*Caracara cheriway*; hereafter ''caracaras''), but has not been correlated to aggressor or receiver roles during agonistic contests. The cere of a caracara is a highly vascularized large patch of bare skin extending from the proximal edge of the beak to below the eye on both sides of the face (Negro et al. 2006). The cere is typically described as orange (Wheeler and Clark 1999) or orange-yellow to red (Ferguson-Lees and Christie 2001), but these colors are typical only of adult caracaras at rest (Morrison and Dwyer 2012). These colors do not completely describe the range of cere colors of either immature or juvenile caracaras at rest, or of any caracaras during some activities. Rather, when a caracara is threatened or frightened, the cere has been described as becoming pale blue, pale yellow, or dark yellow, depending on the age of the

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individual (see Methods; Lyons 1984, Morrison and Dwyer 2012), and these color changes occur within seconds (Brown and Amadon 1968, Vuilleumier 1970). To change the color of the cere, arterial blood flows rapidly through surface capillaries coloring the skin red, or is withheld from surface capillaries, allowing the lighter color of subcutaneous tissue to be visible (Negro et al. 2006).

Crested Caracaras are neotropical Falconids distributed from northern South America to the southwestern United States and southern Florida (Ferguson-Lees and Christie 2001). Nonbreeding caracaras are highly social, and are known to forage in groups and share communal roosts (Rodríguez-Estrella and Rivera-Rodríguez 1992, Skoruppa and Lee 2008, Morrison and Dwyer 2012). While researching the ecology of nonbreeding Caracaras (Dwyer 2010, Dwyer et al. 2012, 2013), I observed the rapid changes in cere colors (Fig. 1) described in Brown and Amadon (1968), Vuilleumier (1970), and Negro et al. (2006). I noticed individuals engaged in agonistic interactions often had different cere colors, and by observing uniquely marked caracaras, I verified that the same individuals often had different cere colors in different interactions, even when those interactions were only seconds apart.

Negro et al. (2006) hypothesized cere color could serve as a quick and quickly reversible signal visible to nearby conspecifics, but the hypothesis has not been quantitatively investigated in wild caracaras. I predicted that if a signaling hypothesis is correct, cere colors displayed by participants in agonistic interactions should be correlated with the role of participants in interactions (as in Bamford et al. 2010, Blanco et al. 2013).

METHODS

To investigate cere color in caracaras, I recorded cere color during intra- and interspecific agonistic interactions involving an aggressor and a receiver within single-species and mixed-species groups of avian scavengers including at least one caracara. I recorded interactions throughout the species' range in Florida, U.S.A., from approximately 28°30′N at the northern edge of their range, to approximately 26°09′N at the southern edge of their range, and from approximately 82°14′W along the west coast of Florida to 80°14 W along the east coast.

I conducted 30-min continuous observations during which I recorded the outcomes of all observed agonistic interactions between avian scavengers (as in Wallace and Temple 1987, Travaini et al. 1998, Dwyer and Cockwell 2011). I conducted observations from a vehicle parked 70–100 m from interacting individuals, and used 10× binoculars (Zeiss, Jena, Germany), or a 20–60× spotting scope (Nikon, Tokyo, Japan) to view agonistic interactions. I separated observation periods by at least 1 hr or 1 km to minimize the likelihood that I would record interactions involving the same pairs of individuals during multiple observations. As much as possible, I observed interactions at naturally occurring feeding sites, but I also conducted observations at experimentally placed carrion, where approximately 2/3 of observations were collected (as in Wallace and Temple 1987, Travaini et al. 1998, Dwyer and Cockwell 2011). Carrion consisted of cottontail rabbit (*Sylvilagus floridanus*), feral pig (*Sus scrofa*), nine-banded armadillo (*Dasypus novemcinctus*), northern raccoon (*Procyon lotor*), and Virginia opossum (*Didelphis virginiana*) carcasses found dead along roads within the study area.

I distinguished between high-intensity and low-intensity interactions as in Dwyer and Cockwell (2011). In high-intensity interactions, the identity of both the aggressor and the receiver were clearly based on physical contact via biting or striking with the foot or wing, or based on pursuit by foot or in flight. In low-intensity interactions, the aggressor was clear, but the receiver sometimes was not. For instance, a caracara carrying out a Head-back Display (Morrison and Dwyer 2012) while standing over a carcass may have been signaling possession of the carcass to a particular individual, or to all individuals nearby. In these cases, I recorded the cere color of the bird directly in front of the signaling bird. If no bird was directly in front of the signaling bird, I recorded the cere color of the nearest bird. These records could be misleading if the behaviors were directed at a different individual than what I recorded. To prevent potentially incorrect attribution of receivers in low-intensity interactions from influencing overall results, I analyzed high-intensity and low-intensity interactions separately.

Each time I observed an agonistic interaction, I recorded the aggressor and receiver species, and the age class and cere color of the caracara(s) involved. I recorded cere color as interactions occurred. I classified caracara ages as juvenile (streaked breast), immature (breasts of mixed streaks and bars), and adult (barred breasts; Wheeler and Clark 1999, Dwyer et al. 2012, 2013). I recorded juvenile caracaras with white, light blue, pink, or orange ceres. I

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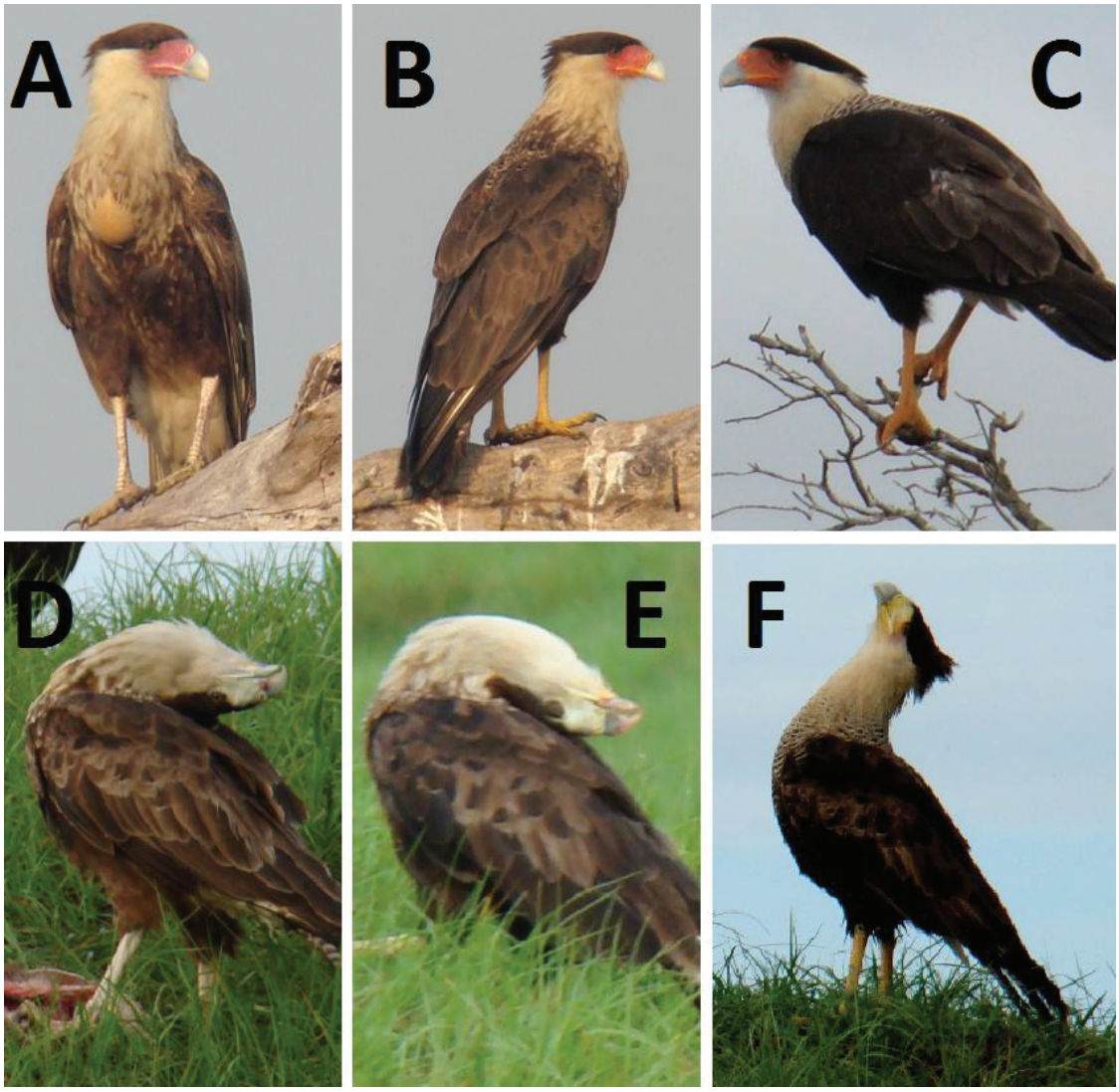


Figure 1. Cere colors of Crested Caracaras. A–C show dark ceres at rest: (A) juvenile; (B) immature; (C) adult. D–F show light ceres during Head-back Displays (an agonistic display): (D) juvenile; (E) immature; (F) adult. All photos by J.F. Dwyer.

recorded immature caracaras with white, pale yellow, pink, or red ceres, and adult caracaras with yellow, dark yellow, orange, or red ceres. Ten assistants helped record agonistic interactions over 33 mo. Each assistant was trained to identify agonistic interactions identically, and to record cere color as interactions occurred.

For analyses, I pooled light colors and dark colors of ceres within age classes. I pooled juveniles with white or light blue ceres (light), and juveniles with pink or orange ceres (dark). I pooled immatures with white or pale yellow ceres (light), and pink or red ceres (dark), and I pooled adults with yellow or dark yellow ceres (light), and orange or red ceres (dark). Consistently across age classes, light-colored ceres matched the leg color of each individual caracara, and because caracaras' legs do not change color facultatively, these colors indicated integument base colors. Leg colors do change non-facultatively with age, from pale blue as nestlings, to pale yellow

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as juveniles, to dark yellow as adults (Morrison and Dwyer 2012). Pooling slight differences in cere color corrected for variability in interpretation of cere colors among observers, corrected for differences in the base color of the integument of individual birds, and grouped birds into categories of flushed and not flushed consistent with previous studies of facial flushing in raptors (Negro et al. 2006, Bamford et al. 2010, Blanco et al. 2013).

I used individual agonistic interactions as the sampling unit. This could lead to lack of independence among some interactions because I could not tell for certain whether I had recorded data from a particular dyad previously. However, because groups often included hundreds of potential dyads, and sampling periods were separated by hundreds of km and across multiple years, the potential for lack of independence between a small number of the agonistic interactions is likely to have minimal effect on the conclusions drawn.

I used χ^2 goodness of fit tests to identify whether one class of participants (e.g., adult caracaras with light ceres) was the aggressor in more interactions than expected vs. other classes of participants (e.g., juvenile and immature caracaras with dark ceres). This approach assumed null hypotheses that each class of participants would be the aggressor in proportion to the occurrence of interactions. I applied Bonferroni corrections for multiple comparisons. Given an initial critical value of $\alpha = 0.05$, for the 18 comparisons made, I considered $\alpha = 0.003$ to indicate statistical significance.

RESULTS

From July 2006 through March 2009, I conducted 149 30-min group observations. Groups included up to 46 caracaras ($\bar{x} = 13.4$, SD = 6.9), and total group sizes ranged from 2–119 individuals ($\bar{x} = 23.4$, SD = 19.0). Other scavengers observed were American Crows (*Corvus brachyrhynchos*), Bald Eagles (*Haliaeetus leucocephalus*), Black Vultures (*Coragyps atratus*), and Turkey Vultures (*Cathartes aura*). I recorded 2586 agonistic interactions in which I could identify the cere colors and ages of both caracaras involved in an intraspecific interaction ($n = 1160$), or in which I could identify the cere color and age of the single caracara involved in an interspecific interaction ($n = 1426$). These included 752 high-intensity intraspecific interactions and 408 low-intensity intraspecific interactions, and 734 high-intensity interspecific interactions, and 692 low-intensity interspecific interactions, respectively.

For intraspecific interactions, I recorded 66 interactions involving two adult caracaras, 46 interactions involving two immature caracaras, and 277 interactions involving two juvenile caracaras. In these cases the aggressor had a light-colored cere and the receiver had a dark-colored cere in 268 of 274 (98%; 95–99%; $\chi^2 = 248.62$, df = 1, $P < 0.0001$) high-intensity interactions, and 118 of 124 (95%; 90–98%; $\chi^2 = 99.36$, df = 1, $P < 0.0001$) low-intensity interactions. Within age classes, light-colored ceres correlated with being the aggressor in intraspecific agonistic interactions.

I recorded 390 interactions involving an adult caracara and either an immature or juvenile caracara. In these cases, adults were the aggressor in 151 of 243 (62%; 56–68%; $\chi^2 = 13.84$, df = 1, $P = 0.0002$) high-intensity interactions, and 102 of 147 (69%; 62–75%; $\chi^2 = 20.58$, df = 1, $P < 0.0001$) low-intensity interactions. I recorded 225 interactions involving one immature caracara and one juvenile caracara. In these cases, immatures were the aggressor in 40 of 161 (25%; 19–32; $\chi^2 = 39.76$, df = 1, $P < 0.0001$) high-intensity interactions, and 14 of 64 (22%; 14–33%; $\chi^2 = 19.14$, df = 1, $P < 0.0001$) low-intensity interactions. Across age classes, adult caracaras were consistently aggressors in agonistic interactions with younger individuals, but immature caracaras were not consistently aggressors in agonistic interactions with juveniles. The aggressor in intraspecific interactions including individuals of different age classes had a light-colored cere and the receiver had a dark-colored cere in 668 of 752 (85%; 81–87%; $\chi^2 = 451.98$, df = 1, $P < 0.0001$) high-intensity interactions, and 211 of 284 (74%; 69–79%; $\chi^2 = 66.08$, df = 1, $P < 0.0001$) low-intensity interactions. Across age classes, light-colored ceres correlated with being the aggressor in agonistic interactions.

In interspecific agonistic interactions, caracaras were the aggressor in 16 of 17 interactions with American Crows (94%; 73–99%; $\chi^2 = 11.52$, df = 1, $P = 0.0007$) and the receiver in 37 of 38 interactions with Bald Eagles (99%; 87–100%; $\chi^2 = 32.24$, df = 1, $P < 0.0001$). Separate analyses of cere color and interaction intensities were precluded by small sample size for these two species. Caracaras with light ceres were the aggressors in 98 of 110 high-intensity interactions (89%; 82–94%; $\chi^2 = 65.68$, df = 1, $P < 0.0001$), and 88 of 92 low-intensity interactions with Black Vultures (96%; 89–98%; $\chi^2 = 74.88$, df = 1, $P < 0.0001$). Caracaras with light ceres were the aggressors in 119 of 147 high-intensity

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interactions (81%; 74–86%; $\chi^2 = 55.10$, df = 1, $P < 0.0001$), and 158 of 195 low-intensity interactions with Turkey Vultures (81%; 75–86%; $\chi^2 = 73.84$, df = 1, $P < 0.0001$). Caracaras with dark ceres were the aggressors in 39 of 57 interactions with Black Vultures (68%; 55–79%; $\chi^2 = 7.02$, df = 1, $P = 0.008$), and 28 of 57 interactions with Turkey Vultures (49%; 37–62%; $\chi^2 = 0.00$, df = 1, $P = 1$). Across species, caracaras were consistently aggressors in interactions with American Crows regardless of cere color, were consistently the aggressors in interactions with Turkey Vultures and Black Vultures only when displaying light cere colors, and were consistently receivers in interactions with Bald Eagles.

DISCUSSION

Caracaras can change the color of their cere within seconds (Brown and Amadon 1968, Vuilleumier 1970, Negro et al. 2006). Caracaras were historically understood to show a light cere when threatened and a dark cere shown when at rest (Lyons 1984, Morrison and Dwyer 2012), but what constituted a threat had not been defined. Negro et al. (2006) hypothesized excited caracaras would interrupt blood flow to the cere, revealing the light color of the underlying integument but were precluded by sample size from speculating which caracaras in intraspecific and interspecific interactions might be categorized as excited. Thus, correlations between cere color and roles during agonistic interactions had been hypothesized but not previously investigated. I predicted that if a signaling hypothesis is correct, cere color of the participants in agonistic interactions should be correlated with the role of participants in interactions (as in Bamford et al. 2010, Blanco et al. 2013). I found cere colors were consistently light across age classes when caracaras acted as the aggressors in intraspecific or interspecific agonistic interactions and consistently dark when caracaras were receivers of intraspecific or interspecific aggression. These patterns were consistent across high-intensity and low-intensity interactions, lending credibility to my interpretations of low-intensity interactions. My data support Negro et al.'s (2006) signaling hypotheses and refine our understanding of that hypothesis by specifically characterizing which caracaras interrupt blood flow during contests, likely acting as a signal of an individual's willingness to terminate, continue, or escalate an agonistic interaction.

The ecology of caracaras may provide some insight into these correlations. Negro et al. (2006) hypothesized that large-bodied, dark-plumaged species in warm environments, like caracaras, initially evolved and used highly vascularized skin patches to dissipate body heat, and secondarily superimposed a signaling system onto this thermoregulatory process. If true, then cere colors characteristic of individuals at rest (passively avoiding agonistic interactions), might also be displayed by individuals seeking to be at rest (actively avoiding agonistic interactions), consistent with my observations. In contrast, Lappet-faced Vultures display dark heads when aggressive and light heads when subordinate (Bamford et al. 2010), and Andean Condors show bare skin full of blood when dominant (Blanco et al. 2013). Apparently, superimposition of a signaling system on a thermoregulatory process does not require evolution of identical signaling conventions among convergently evolved species. Future research should explore differences in the coloration of bare skin of avian scavengers engaged in agonistic interactions to identify patterns in phylogeny or geography related to whether species display bare skin full of blood or bare skin drained of blood when aggressive. Such research would be particularly interesting because Old World vultures, New World vultures and caracaras are very distant phylogenetically and spatially, but have similar carrion-eating habits, sociality, bare skin on the head, and occupancy of hot habitats (Ferguson-Lees and Christie 2001).

Potential benefits of signaling are well developed theoretically (Parker 1974, Bower 2005, McGregor 2005). For the losing individual, signaling submission may facilitate the rapid conclusion of a contest, thus limiting the risk of injury (Lehner et al. 2011). For the winning individual, concluding a contest as quickly as possible minimizes time and energy costs, allowing the winner to consume defended resources or redirect aggression to another receiver. Dwyer and Cockwell (2011) noted that in Southern Caracaras (*Caracara plancus*) receivers of agonistic interactions usually retreated <1 m from the aggressor and then resumed pre-aggression activity without receiving additional aggression. For Crested Caracaras in Florida, I did not quantify behaviors of participants after aggressions ended, but can anecdotally report observations similar to those of Dwyer and Cockwell (2011). In Florida, contest winners typically fed at the contested portion of a carcass or perched on the location from which the receiver was supplanted. Receivers typically shifted <1 m to feed at an alternate location on the same carcass or shifted

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<3 m to an adjacent perch. As in Dwyer and Cockwell (2011), receivers that deferred to aggressors resumed prior activities within seconds, and receivers that contested aggressors often engaged in escalating aggression until a clear loser was chased from the area or pinned on its back on the ground with the contest winner striking the loser with bill, talons, and wings. Thus, terminating aggression prior to incurring an injury may be important to Crested Caracaras receiving agonistic interactions.

Dominance among avian scavengers is often defined in terms of proportions of contests won or lost by individuals with specific attributes (age, sex, species, etc.; Wallace and Temple 1987, Bamford et al. 2010, Dwyer and Cockwell 2011). My observations verified that adult caracaras were dominant over younger birds, consistent with hierarchies of avian scavengers in general and caracaras in particular throughout Central and South America (Travaini et al. 1998, Dwyer and Cockwell 2011, Blanco et al. 2013). Caracaras displaying light ceres were dominant over caracaras displaying dark ceres. Age and cere color reinforced one another in adult caracaras, such that adult caracaras typically displayed light-colored ceres when engaged in contests with younger birds and consistently won those contests. As in Andean Condors (Blanco et al. 2013), color changes were not limited to adults. Specific cere colors consistently correlated with aggressors and receivers in mixed-age contests involving immature and juvenile caracaras such that individuals displaying light ceres tended to win contests against individuals displaying dark ceres regardless of whether the aggressor was the immature or the juvenile.

Caracaras were subordinate to much larger Bald Eagles and, dominant over much smaller American Crows, regardless of the cere color or age class of the caracara involved. Caracaras displaying light ceres were dominant over Black Vultures and Turkey Vultures even though both vulture species outweigh caracaras (Ferguson-Lees and Christie 2001). Caracaras displaying dark ceres were equally ranked with Black Vultures and Turkey Vultures. Caracaras are unique in that they have historically been identified as dominant to Turkey Vultures (1800 g; Buckley 1996, Rodríguez-Estrella and Rivera-Rodríguez 1992) and dominant or equally ranked to Black Vultures (2000 g) in interspecific interactions (Travaini et al. 1998). Variation in cere color likely explains some of the variation in previous research on interactions between caracaras and vultures. My findings are consistent with previous studies with respect to intraspecific age-related dominance in avian scavengers. Typically, among avian scavengers larger birds are dominant over smaller birds both within and between species, and older birds rank higher than younger birds within species (Rodríguez-Estrella and Rivera-Rodríguez 1992, Travaini et al. 1998, Dwyer and Cockwell 2011).

The correlations identified here rely on human observer's perception of avian coloration during contests. Conclusions drawn here would be more robust if cere colors were objectively quantified and recorded for the same individuals immediately before, during, and immediately after contests. This approach would document color changes, not simply correlations, and provide substantially stronger support for the Negro et al. (2006) signaling hypothesis.

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