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EVOLUTION OF COMMUNAL ROOSTING: A SOCIAL REFUGE–TERRITORY PROSPECTING HYPOTHESIS

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ABSTRACT.—Avian communal roosts provide insight into evolution and serve as focal points for conservation. Nonbreeding Crested Caracaras (*Caracara cheriway*; hereafter caracaras) use communal roosts, but evolutionary implications have not been explored. Though nonbreeding caracaras are nonmigratory, the scientific literature fails to explain seasonal differences in their movement and survival concurrent with seasonal consistency in their habitat and social ecology. In the Social Refuge–Territory Prospecting hypothesis we propose, socially subordinate nonbreeding caracaras precluded from breeding by habitat limitation use communal roosts as social refuges to avoid aggression from dominant territory holders during nonbreeding seasons, and engage in territory prospecting during breeding seasons. Communal roosts thus become central places from which to forage not for food, but for a breeding territory. Because foraging gains are stored as remembered information, competition costs resulting from public information are preempted. For the Social Refuge–Territory Prospecting hypothesis to be valid, two criteria need to be met. First, communal roost use needs to be higher during nonbreeding seasons. Second, a measure of fitness needs to be used to evaluate the hypothesis as an evolutionarily stable strategy. To meet these criteria, in this study we report that numbers of nonbreeding caracaras using a communal roost in Florida are higher during nonbreeding seasons (mean = 111.8 individuals / night) than during breeding seasons (mean = 60.7 individuals / night) as counted from August 2006–April 2009 ($n = 407$ counts). We also compare differential survival by season from previous work to demonstrate that by limiting exploratory movements to times when prospecting is most informative, nonbreeding caracaras balance maximizing survival against the likelihood of securing a breeding territory. Our hypothesis provides a unifying explanation for otherwise unexplained paradoxes in the ecology of nonbreeding caracaras, and may be useful in guiding conservation and expanding our understanding of the ecology of other communally roosting birds.

KEY WORDS: *Crested Caracara*; Caracara cheriway; *floater*; *habitat limitation*; *information center hypothesis*; *nonbreeding*; *public information*.

EVOLUCIÓN DE LOS DORMIDEROS COMUNALES: UNA HIPÓTESIS PROSPECTIVA SOBRE REFUGIO SOCIAL-TERRITORIO

RESUMEN.—Los dormideros comunales de aves proporcionan información sobre la evolución y sirven como puntos focales para la conservación. Los individuos no reproductivos de *Caracara cheriway* (en adelante caracaras) usan dormideros comunales, pero las implicancias evolutivas no han sido exploradas. Aunque los caracaras no reproductivos no son migratorios, la literatura científica no explica las diferencias estacionales en su movimiento y supervivencia concurrentes con la consistencia estacional en su hábitat y ecología social. La Hipótesis Prospectiva de Refugio Social-Territorio propone que los caracaras no reproductivos

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socialmente subordinados, excluidos de la cría por limitantes de hábitat, utilizan dormideros comunales como refugios sociales para evitar la agresión de los individuos dominantes, poseedores de territorio durante la estación no reproductiva, y participan en la prospección del territorio durante las estaciones de cría. Los dormideros comunales se convierten así en lugares centrales para buscar, no alimento, sino un territorio reproductivo. Debido a que la ganancia de las búsquedas se almacena como información registrada, se anticipan los costos de competencia resultantes de la información pública. Para que la Hipótesis Prospectiva de Refugio Social-Territorio sea válida, se deben cumplir dos criterios. Primero, el uso de dormideros comunales debe ser mayor durante las estaciones no reproductivas. Segundo, se debe usar una medida de eficacia biológica para evaluar la hipótesis como una estrategia evolutivamente estable. Para cumplir con estos criterios, en este estudio constatamos que la cantidad de caracaras no reproductivos que utilizan un dormidero comunitario en Florida es mayor durante las estaciones no reproductivas (media = 111.8 individuos/noche) que durante las estaciones reproductivas (media = 60.7 individuos/noche), contados de agosto 2006 a abril 2009 (n = 407 conteos). También comparamos la supervivencia diferencial por estación a partir de trabajos previos para demostrar que al limitar los movimientos exploratorios a los tiempos cuando la prospección es más informativa, los caracaras no reproductivos equilibran la maximización de la supervivencia con la probabilidad de asegurarse un territorio reproductivo. Nuestra hipótesis proporciona una explicación unificadora para las paradojas, de otro modo inexplicables, sobre la ecología de los caracaras no reproductivos, y puede ser útil para guiar la conservación y expandir nuestra comprensión sobre la ecología de otras aves que usan dormideros comunales.

[Traducción del equipo editorial]

The evolution of avian communal roosting has been a focal point for study and debate since Ward and Zahavi (1973) first presented what would become known as the Information Center Hypothesis (ICH; Bijleveld et al. 2010). The ICH proposed that avian communal roosts served as social centers where birds actively recruited peers to foraging areas, and proposed this as the primary mechanism driving the evolution of communal roosting. There are two problems with the ICH. First, it relies on reciprocal altruism to explain why knowledgeable individuals choose to incur the costs of increased competition resulting from recruiting peers to foraging areas (Bijleveld et al. 2010). To be an evolutionarily stable strategy, reciprocal altruism requires multiple interactions among pairs of individuals (Suzuki and Akiyama 2008), an uncertain benchmark when communal roost composition is dynamic (Conklin and Colwell 2008). In the absence of demonstrable altruism, some complementary factor, such as intraspecific competition (Marzluff et al. 1996, Wright et al. 2003), predation (Krause and Ruxton 2002, Rogers et al. 2006) or inclusive fitness (Rabenold 1986) is needed to explain the behavior of knowledgeable birds at communal roosts. Second, the various life-history strategies of the wide spectrum of communally roosting birds makes it unlikely that a single explanation can encompass the evolution of communal roosting in all species. Though support for the ICH has been limited, the cost-benefit approach with which the ICH has been evaluated remains an essential tool in developing evolutionary hypotheses (Bijleveld et al. 2010).

Given the poor fit of the ICH to various species, many more hypotheses for the evolution of communal roosting have been proposed. For example, the evolution of communal roosting in birds has been attributed to fitness increases related to avoidance of competition with socially dominant conspecifics (Ferrer and Harte 1997, Beauchamp 1999, Penteriani et al. 2008), obtaining information about the distribution and abundance of food (Buckley 1996), avoidance, detection, or saturation of predators (Krause and Ruxton 2002, Rogers et al. 2006, Conklin and Colwell 2008), opportunities to find mates among the communal roosting population (Blanco and Tella 1999), identification of vacant territories (Blanco and Tella 1999), and collaborative thermoregulation (Krause and Ruxton 2002, Chappell et al. 2016). Each hypothesis appears to apply well to particular species, and once in place, the evolutionary driver of communal roosting in any given species does not preclude secondary benefits consistent with other hypotheses (Krause and Ruxton 2002).

A weakness in many existing hypotheses is the unstated assumption that individuals using communal roosts perceive the roost positively, i.e., that individuals want to be at the communal roost. In contrast to this, we begin from a hypothesis that in some cases individuals may not view a communal roost positively, but may use it anyway to make the best of a bad situation. To illustrate this, we begin as

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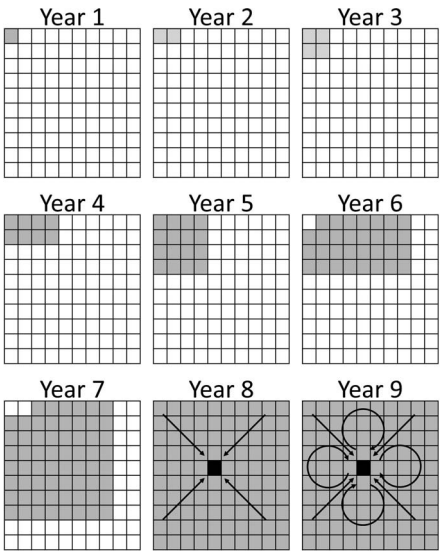


Figure 1. A simplified thought experiment illustrates formation of a communal roost in a closed habitat patch where one breeding pair is introduced and breeding territories are defended for 5-yr lifespans. Gray cells: occupied territories. White cells: vacant territories. Black cell: communal roost. Straight arrows: accumulation of nonbreeders at a communal roost. Circular arrows: prospecting for territories by nonbreeders from a communal roost. In this scenario, nonbreeders use the communal roost because no better options (breeding or emigration) exist.

Clobert et al. (2001) did, with a thought experiment. Consider the following thought experiment for a hypothetical species which uses communal roosts. Imagine a closed and isolated patch of habitat 10 km^2, similar conceptually to the Crested Caracaras' (*Caracara cheriway*) range in the Florida peninsula where neither immigration nor emigration occurs (described below). In the thought experiment, breeding pairs of species X occupy 1-km^2 breeding territories year-round from the second year of life through the sixth year of life, so breed for 5 yr, and then die. Breeding occurs annually, and territories abut one another so no intra-territorial spaces occur. If one breeding pair is introduced into the habitat, then assuming an ideal free distribution (Fretwell and Lucas 1970), all 100 of the 1-km^2 breeding territories will be occupied within 8 yr (Fig. 1). Thereafter, most of the additional young produced cannot occupy a breeding territory and none can emigrate. They must go somewhere. One solution might be for the nonbreeding individuals to aggregate at a single location, regardless of age or physiological breeding potential, overwhelming the territorial defense of a single breeding pair, and forming a communal roost. None of the individuals using the communal roost necessarily perceives their residency there as positive. They would presumably rather establish breeding territories of their own, but they have no viable path to do so. In this way communal roosting could evolve as a response to territoriality and habitat limitation. Thereafter, proximate secondary foraging benefits could develop, but these benefits would not ultimately be responsible for the evolution of communal roosting in this scenario.

A second weakness of many hypotheses for the evolution of communal roosting is that the hypotheses assume the resource of interest is food, that the food in question is patchily distributed and ephemeral, and that successful foragers can be distinguished from unsuccessful foragers. If the limiting resource is not food, but instead breeding territories, then the resource may not be ephemeral, successful foragers will gain information that is stored in memory, and information gained will not be available as public information to their communally roosting competitors. A third weakness of many hypotheses for the evolution of communal roosting is that they focus on migratory species breeding in the northern hemisphere, and thus avoid the need to explore or explain seasonal differences in communal roost use in breeding and wintering areas.

Though the movements of individuals, and the causes and consequences of those movements are some of the most-studied concepts in ecology, they remain poorly understood (Clobert et al. 2001), perhaps due in part to weaknesses in existing hypotheses and their underlying assumptions. Re-evaluations of the assumptions that (1) communal roosts may in some cases be occupied more-or-less involuntarily, (2) the limiting resource driving communal roosting may not be ephemeral, and (3) seasonal differences in communal roost use are related to migration form the basis for the alternate evolutionary explanation for communal roosting proposed here.

The Social Refuge–Territory Prospecting Hypothesis. Here, we propose the Social Refuge–Territory Prospecting hypothesis to explain the evolution of communal roosting in a nonmigratory species subject to year-round territoriality and habitat limitation. We define social refuges as locations that

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socially subordinate individuals occupy to avoid fitness-reducing interactions with socially dominant conspecifics. The term social refuge consolidates various observations into a unified concept. For example, temporary settlement areas (e.g., Penteriani et al. 2008, Balbontín and Ferrer 2009, Tanferna et al. 2013), temporary settling areas (e.g., Ferrer 1993, Ferrer and Harte 1997), staging areas (Mellone et al. 2011), and dispersal areas (Moleón et al. 2011) each are slightly different ways of conceptualizing spatial arrangements of socially subordinate nonbreeding birds and socially dominant breeding birds. Social refuges also may occur at territory edges where non-territorial individuals can escape aggression of territory holders by moving into adjacent nonbreeding habitat (Dwyer et al. 2013), or an adjacent territory without that territory-holder immediately noticing (Rohner 1997). Social refuges can include indefensible areas around point subsidies, such as landfills, that create perpetual, abundant, spatially fixed resources (Webb et al. 2004), or around carcasses if the numbers of non-territorial birds overwhelm a territory holder's ability to defend an area (Marzluff et al. 1996). Any of these gatherings can function as social refuges if they facilitate access to resources that otherwise would be defended by a breeding pair of territorial birds.

Communal roosts could develop, and communal roosting evolve, where non-territorial individuals aggregate at social refuges to avoid fitness-reducing consequences of intraspecific conflict with social dominants. A substantial fitness-reducing cost to using a social refuge is that the same mechanisms that prevent territorial defense of the site inherently create a conflict between short-term (survival to breeding) and long-term (breeding) fitness goals, where fitness is defined as a measure of the extent to which an individual contributes genes to future generations (Freeman and Heron 1998). Specifically, staying at the communal roost may be relatively safe, leading to long life, but mostly precludes breeding, either due to insufficient resources to raise offspring, or due to high competitive pressure from communal roost-mates (though inclusive fitness benefits may accrue).

Territory prospecting facilitates nonbreeding individuals gathering information on the local quality of potential future breeding sites (Ponchon et al. 2013), and occurs when reliable information on territory quality is most available, with productivity serving as that information (Boulinier et al. 1996, Boulinier et al. 2008). Prospecting birds evaluate the presence and quality of offspring produced in a territory as an indicator of their own likely success. Prospecting may also provide cues on whether an existing territory holder might be vulnerable to replacement. Thus, prospecting occurs primarily during breeding seasons and can involve relatively large movements across multiple territories by prospecting individuals (Reed et al. 1999, Tobler and Smith 2004, Ward 2005). Other cues, such as an unmated individual of the opposite sex resident within a potential territory, may indicate that a breeding attempt might be possible in a given location, but do not indicate whether that attempt is likely to be successful.

Evaluating the relative quality of specific potential breeding sites (territory prospecting) prior to attempting to occupy a site is hypothesized to be an ideal dispersal strategy if the environment contains a low proportion of high-quality habitat patches, even if doing so is associated with a cost (i.e., loss of a low-quality breeding opportunity; Boulinier and Danchin 1997). This may be particularly true for long-lived species that hold permanent territories throughout their breeding years because holding a high-quality territory for a shorter period may lead to greater lifetime reproductive success than holding a low-quality territory for a longer period.

The Social Refuge–Territory Prospecting hypothesis proposes that seasonal changes in communal roosting reflect seasonal changes in the relative weight of the multiple selective pressures acting on each individual. Specifically, we propose that individuals avoiding year-round territoriality of socially dominant conspecifics (as occurs in Crested Caracaras; described below), should use social refuges during nonbreeding seasons when there is relatively little to be gained from trespassing on breeding territories, and should engage in territory prospecting during breeding seasons when there is much to be gained from trespassing.

Here we examine the behavioral ecology of Crested Caracaras (hereafter caracaras) to examine whether the Social Refuge–Territory Prospecting hypothesis may offer an explanation unifying multiple components of the seasonally asymmetric behavior of nonbreeding individuals of all age classes in this enigmatic species. Caracaras are nonmigratory facultative avian scavengers distributed from central South America to southern North America, with an apparently isolated population in south Florida from which no emigration or immi-

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gration is known to occur (Morrison and Dwyer 2012). Breeding caracaras defend territories year-round and do not use communal roosts (Morrison and Dwyer 2012).

Nonbreeding caracaras are highly social (Dwyer 2014), do not defend territories (Morrison and Dwyer 2012), and use communal roosts extensively (Lasley 1982, Johnson and Gilardi 1996, Dwyer 2010). These nonbreeders include juveniles not capable of breeding (Morrison and Dwyer 2012), immatures apparently capable of breeding though they do so only rarely (Nemeth and Morrison 2002), and floaters persisting in the nonbreeding population for at least 3 yr (Dwyer et al. 2012). Floaters are individuals that are presumably physiologically capable of breeding but which do not hold a territory (Newton and Rothery 2001, Penteriani et al. 2008). In one study of nonbreeding caracaras in Florida, floaters made up an average of 37% (95% CI 32–42%) of nonbreeders occupying communal roosts (Dwyer 2010), persisting for years in a recirculating transient phase of dispersal. The ecology of nonbreeding caracaras is distinctly seasonal, though this seasonality has not been previously explained. Specifically, nonbreeding caracaras have higher survival during breeding seasons than during nonbreeding seasons (Dwyer et al. 2012). Nonbreeding caracaras also move more widely around the species' range during breeding seasons than during nonbreeding seasons (Dwyer et al. 2013), blurring the line between dispersal and migration. To resolve these various unusual life-history traits, we propose that communal roosts function as social refuges to allow nonbreeding caracaras to remain adjacent but external to territories defended by breeding caracaras, and that during breeding seasons, nonbreeding caracaras disperse from these social refuges to prospect for territories.

METHODS

As applied to caracaras, the Social Refuge–Territory Prospecting hypothesis hinges on an assumption that most of the costs and benefits that nonbreeding caracaras balance day-to-day are relatively consistent year-round, and that the only substantial seasonal variation is the relative value of information available from territory prospecting. To evaluate this, we made 13 predictions based on the Social Refuge–Territory Prospecting hypothesis (Table 1). We then reviewed the existing literature on caracaras to identify whether and which of these hypotheses were supported or refuted. A key prediction was that the number of caracaras using a communal roost should be relatively low during breeding seasons when territory prospecting would be beneficial and relatively high during nonbreeding seasons when prospecting offered little benefit. Important to this prediction is an understanding that most (96%) nesting attempts (i.e., egg-laying) in Florida are initiated from October through March (Morrison 1999), with hatching approximately 1 mo after egg-laying, and fledging 2 mo after that (Morrison and Dwyer 2012). Young then remain on natal territories for as little as 2 mo or as many as 10 mo (Morrison and Dwyer 2012), resulting in a trickling, rather than a pulsed entry into the nonbreeding population.

Because no information on year-round communal roost use was available, we tested our prediction of roost use by counting nonbreeding caracaras using a communal roost from August 2006 through April 2009. We conducted these counts from a vantage point with an unobstructed view of the communal roost (*cf.* Sykes 1985, Sweeney and Fraser 1986). During counts, we recorded caracaras entering the communal roost in 1-min intervals relative to sunset (*cf.* Sykes 1985) from 1 hr before sunset until 0.75 hr after sunset. This protocol could have allowed birds to enter the communal roost undetected if they arrived after it became too dark for us to see. We evaluated that possibility via simultaneous visual and signal identification of the arrival of individuals radio-tagged in a related study (Dwyer 2010, Dwyer et al. 2013). This also allowed us to confirm that breeding caracaras with territories nearby did not enter the communal roost, reconfirming our earlier assertion (Morrison and Dwyer 2012).

The communal roost we studied was near the center of the caracara's range in Florida (Fig. 2; Dwyer 2010, Dwyer et al. 2013, Smith et al. 2017), adjacent to the MacArthur Agro-Ecology Research Center near Lake Placid, Florida (27°9′N, 81°12′W). The communal roost was composed of approximately 0.015 ha of Sabal palms (*Sabal palmetto*) embedded in a matrix of pastures, palm hammocks, oak-palm hammocks, seasonal wetlands, and commercial citrus groves typical of caracara habitat (Morrison and Humphrey 2001, Dwyer et al. 2013, Smith et al. 2017). The subtropical study area was characterized by a rainy season (June–September), and a dry season (October–May; Chen and Gerber 1990).

Statistical Analyses. Caracaras in Florida breed year-round, but most nesting occurs during the 6 mo

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Table 1. Predictions supporting the Social Refuge–Territory Prospecting hypothesis.

HYPOTHESIS	PREDICTION	SUPPORT
Social Refuge	Breeding habitat is limited	Morrison and Humphrey 2001
	Breeding caracaras do not use communal roosts	Morrison and Dwyer 2012
	Breeding and nonbreeding caracaras co-exist in overlapping space	Dwyer et al. 2013
	Breeding territories are defended from nonbreeding caracaras year-round	Morrison and Dwyer 2012
	Aggressive encounters occur when nonbreeding birds trespass on breeding territories	Morrison and Dwyer 2012
	Nonbreeding caracaras' survival is lower during breeding seasons	Dwyer et al. 2012
Territory Prospecting	Nonbreeding caracaras are not food limited during any season	Morrison and Pias 2006
	Nonbreeding caracaras are physiologically capable of breeding	Nemeth and Morrison 2002
	Nonbreeding caracaras trespass more frequently during breeding seasons	Implied from Dwyer et al. 2013
	Nonbreeders' home ranges are greater during breeding seasons than nonbreeding seasons	Dwyer et al. 2013
	Nonbreeding birds seek undefended areas when there is little benefit to be gained by trespassing	Typical of territory prospecting[a]
	Nonbreeding caracaras acquire territories where they engage in territory prospecting	Typical of territory prospecting[b]
	Nonbreeding caracaras show seasonal variation in communal roosting	Presented here

[a] Boulinier et al. (1996), Reed et al. (1999), Ponchon et al. (2013).
[b] Blanco and Tella (1999).

from October through March (Morrison 1999). As in Dwyer et al. (2012, 2013), we defined October through March as the breeding season, and December and January, when 61% of nests are initiated, as the peak of the breeding season. We defined April through September as the nonbreeding season. These assignments allowed us to compare counts at the communal roost during the peak of breeding seasons to counts during the tails of breeding seasons, and to counts during nonbreeding seasons. We used analysis of variance (ANOVA) to explore seasonal and annual variation in the number of caracaras counted at the communal roost each month. For these analyses, we calculated the average number of caracaras observed entering the communal roost across counts within each month, and used monthly averages in ANOVAs. This helped reduce pseudoreplication of counts on adjacent days and reduced the influence of large or small outlying counts, though some autocorrelation inevitably persists in data where some of the same birds used the roost for long periods. We considered statistical results significant at $P \leq 0.05$.

RESULTS

We identified 13 predictions that must be met for the Social Refuge–Territory Prospecting hypothesis to be supported. Of those, 12 were evaluated based on published literature, and one is tested here.

Hypotheses Supported by Existing Literature. With regard to the social refuge half of our hypothesis, the breeding habitat of caracaras in Florida is limited (Morrison and Humphrey 2001) and defended year-round by territorial breeders (Morrison and Dwyer 2012) that do not use communal roosts (Morrison and Dwyer 2012). Breeding and nonbreeding caracaras coexist in overlapping space however (Dwyer et al. 2013), which leads to intraspecific aggression when nonbreeding birds trespass on breeding territories (Morrison and Dwyer 2012). Survival of nonbreeding caracaras is reduced during breeding seasons compared to nonbreeding seasons (Dwyer et al. 2012). Specifically, based on year-round radiotelemetry, monthly survival (mean, SE) is highest during nonbreeding seasons (0.995, 0.004), lower during the tails of breeding seasons (0.984, 0.007), and

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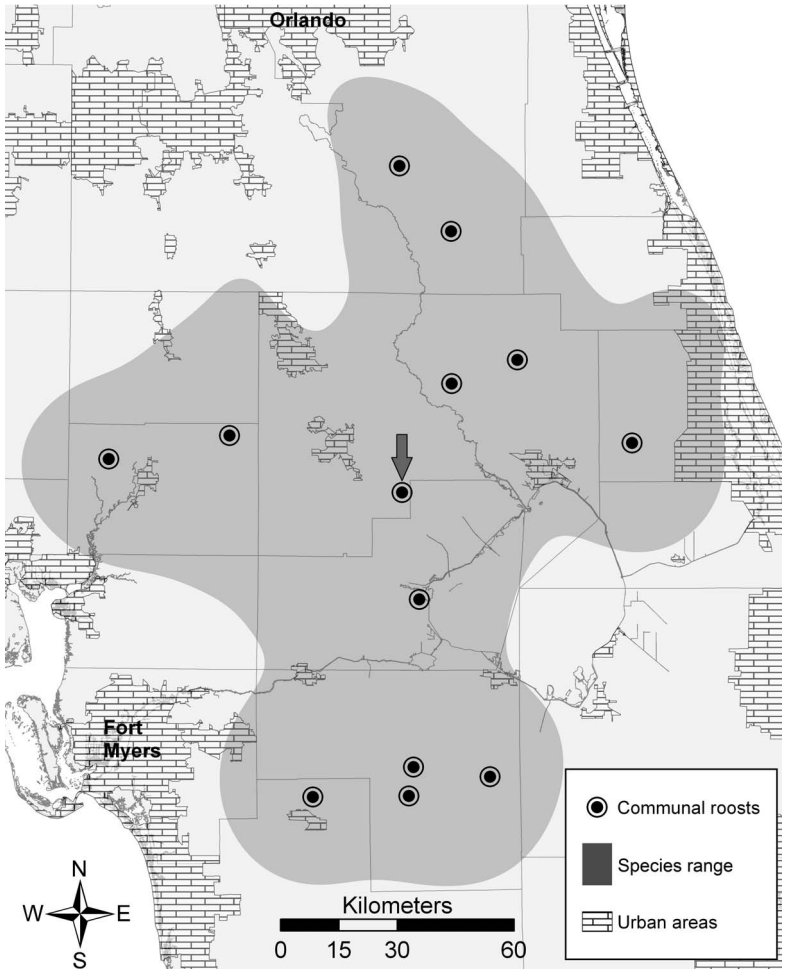


Figure 2. Locations of communal roosts used by caracaras in Florida (Dwyer 2010). Grey arrow indicates the communal roost near the center of the species' range where count data were collected August 2006 through April 2009.

lowest during the peak of breeding seasons (0.953, 0.019).

With regard to the territory prospecting half of our hypothesis, nonbreeding caracaras are physiologically capable of breeding (Nemeth and Morrison 2002). The pellets of nonbreeders consistently contain lower-quality forage than the pellets of breeders (Morrison et al. 2008), indicating nonbreeders occupy lower-quality habitats year-round (Morrison and Pias 2006), but suggesting nonbreeders are not food-limited during breeding seasons, i.e., not wandering more widely during breeding seasons in search of food (Dwyer et al. 2013). Nonbreeding caracaras use home ranges that are approximately five times larger during breeding seasons than during nonbreeding seasons, apparently because trespassing occurs more frequently during breeding seasons in caracaras (Dwyer et al. 2013).

Hypothesis Tested Here. From 9 August 2006 through 17 April 2009 ($n = 407$ counts, mean = 1 count/2.4 d), we counted nonbreeding caracaras at a communal roost that had not been documented prior to this study (Fig. 3). We found nonbreeding caracaras were present year-round during each count for 33 mos (nightly mean = 91 individuals, median = 73, SD = 62, SE = 3, min = 6, max = 304). Our counts included 6 mo during the peak of breeding seasons, 12 mo during the tails of the breeding seasons, and 15 mo during nonbreeding

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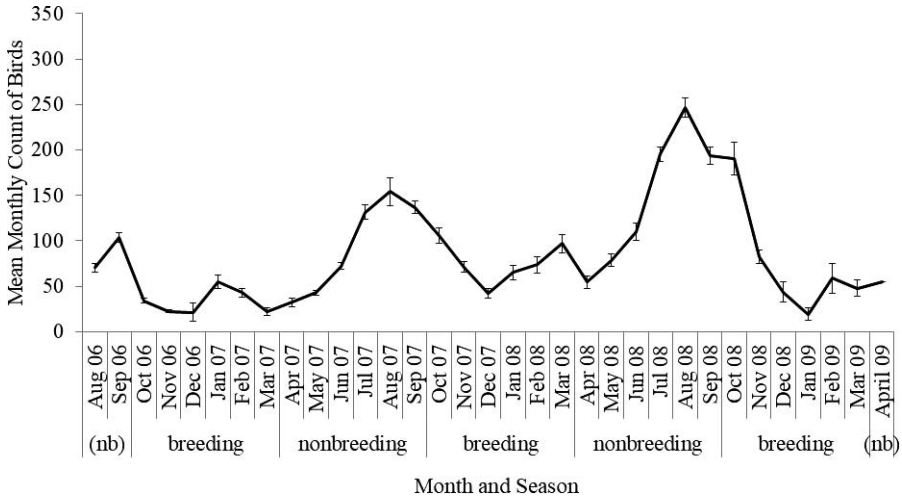


Figure 3. Mean monthly counts of Crested Caracaras at a communal roost near Lake Placid, Florida. Bars indicate standard errors within months. The breeding and nonbreeding (nb) seasons for Crested Caracaras are denoted on the x-axis $n = 407$ counts. Data collected August 2006 through April 2009.

seasons. Average monthly counts of nonbreeding caracaras were lowest (mean = 40.9, SD = 7.4) in December and January ($F_{2,30} = 4.53$, $P = 0.019$) during the peak of the breeding season, higher during the tails of the breeding season (October, November, February, and March; mean = 80.1, SE = 15.6), and highest during the nonbreeding season (April through September; mean = 109.9, SE = 17.3).

Every radio-tagged nonbreeding caracara that arrived at the communal roost was confirmed with a visual observation ($n = 855$ observations of 19 radio-tagged individuals, mean = 45.1 observations per individual, min = 2, max = 161). These radio-tagged birds did not consistently share the communal roost however, with some birds using it on some nights, and others on other nights, indicating dynamic communal roost composition. During counts at the communal roost, we never detected breeding caracaras that had been radio-tagged in the area.

DISCUSSION

Ward and Zahavi (1973) postulated the ICH to explain central place foraging for food. Because neither the ICH, nor other existing hypotheses for the evolution of communal roosting adequately explained all aspects of communal roosting in nonbreeding caracaras, we developed the Social Refuge–Territory Prospecting hypothesis. Under the Social Refuge–Territory Prospecting hypothesis, communal roosts may serve as social refuges and may also function as central places from which nonbreeders forage not for food, but for territories in a prospecting context.

To propose our Social Refuge–Territory Prospecting hypothesis as a driver of the evolution of communal roosting in nonbreeding Crested Caracaras, we must offer a link between the behavior we report and the fitness implications for individuals undertaking that behavior. Previously published differences in seasonal survival of nonbreeding caracaras (Dwyer et al. 2012) facilitates such an assessment. Nonbreeding caracaras' monthly survival is highest during nonbreeding seasons when they disproportionately use communal roosts (April–September), lower during the tails of the breeding season (October, November, February, March), and lowest during the peak of breeding (December–January). Actual annual survival is intermediate between what might be expected if nonbreeding caracaras remained at communal roosts year-round and what survival might be if nonbreeding caracaras avoided communal roosts year-round (Fig. 4). Comparing these survival rates year-round illustrates that a nonbreeding caracara using a communal roost year-round would likely survive longer (probability of survival to 5 yr > 0.80), but would be unlikely to identify and secure a breeding territory. A nonbreeding caracara engaged in territory prospecting

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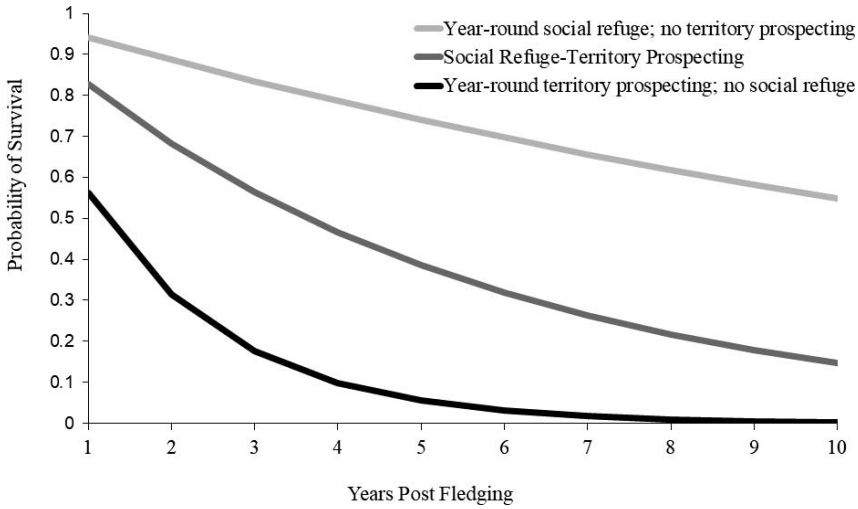


Figure 4. Actual probability of survival for nonbreeding caracaras (from Dwyer 2012; middle line). Predicted probability of survival for nonbreeding caracaras if survival rates during nonbreeding seasons (from Dwyer 2012) are extrapolated year-round (top line). Predicted probability of survival for nonbreeding caracaras if survival rates during breeding seasons (from Dwyer 2012) are extrapolated year-round (bottom line).

year-round would not likely live very long (probability of survival to 5 yr < 0.10). The Social Refuge–Territory Prospecting hypothesis unifies documented seasonal variation in survival with fitness decisions by demonstrating an evolutionarily stable strategy wherein nonbreeding caracaras increase the risks they take only when the likelihood of a fitness payoff is high (probability of survival to 5 yr approximately 0.40). Individuals balancing these conflicting costs and benefits have the best chance of maximizing their fitness through surviving long enough to secure a breeding territory.

Food Availability. A potential weakness in our test of the Social Refuge–Territory Prospecting hypothesis is that we did not directly evaluate food availability across seasons. If food were particularly limited during breeding seasons, when nonbreeding caracaras range most widely and die most frequently, then variation in food availability might drive the communal roosting patterns we observed. However, because birds consistently breed during the season when food is most abundant, it is unlikely that there are sufficient food resources for breeding caracaras to not only survive, but also raise young, while nonbreeding caracaras lack sufficient food for basic survival. Instead, Occam's razor would suggest that food is abundant for this generalist forager across breeding classes, and that a failure to recognize this may stem more from the human's inability to conceptualize the reality that animals can act on memories formed during territory prospecting, than from any ecologically relevant obstacle.

Application to Other Species. Spanish Imperial Eagles (*Aquila adalberti*) spend the first 3–5 yr of their lives as non-territorial immatures, occupying temporary settlement areas that are not used by adults (Ferrer and Harte 1997). Adult Spanish Imperial Eagles defend permanent breeding territories, presumably incorporating the highest-quality habitats, while a series of nonbreeding birds use the same temporary settling areas in sequential years (Ferrer 1993). Using the terminology of our hypothesis, immature Spanish Imperial Eagles may be relegated to social refuges while developing to sexual maturity, and then once maturity is reached, they can begin prospecting for breeding territories. Similarly, during the transient phase of dispersal in juvenile Bonelli's Eagles (*Aquila fasciata*), individuals use communal roosts in dispersal areas (Moleón et al. 2011), but also spend large parts of their time exploring surrounding areas, probably with the aim of searching for vacant territories or mates (Balbontín and Ferrer 2009). The on-again-off-again use of communal roosts in temporary settlement areas may be seen as moving back and forth between social refuges and territory prospecting, balancing short-term oscillations in the costs and benefits of the social refuge and territory prospecting. In Short-

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toed Snake-Eagles (*Circaetus gallicus*), immatures use summer staging areas where intraspecific competition is likely lower than within breeding areas (Mellone et al. 2011). In this case, immature birds incapable of breeding may use social refuges to avoid dominant conspecifics.

Some colonial species engage in territory prospecting while breeding, and shift nest sites between breeding seasons based on the success of their neighbors. For example, in Black-legged Kittiwakes (*Rissa tridactyla*; Boulinier et al. 1996, Boulinier et al. 2008), Lesser Kestrels (*Falco naumanni*; Aparicio et al. 2007), Cliff Swallows (*Petrochelidon pyrrhonota*; Brown et al. 2000), and Collared Flycatchers (*Ficedulla albicollis*; Ponchon et al. 2013), nesting individuals are socially dominant at their own nests, but socially subordinate elsewhere throughout the colony. Under the Social Refuge–Territory Prospecting hypothesis, the existing nest site can be viewed as a social refuge from which individuals prospect when evaluating other sites within the colony. No single evolutionary explanation is likely to explain communal roosting in all species engaged in the behavior, but our hypothesis nevertheless appears to have the potential for application beyond caracaras.

Application to Other Communal Roosts. Various types of communal roosts exist. Main roosts (Blanco and Tella 1999), permanent roosts (Sweeney and Fraser 1986), and persistent roosts (Buckley 1999) are used year-round, though there is often high turnover among individuals (Rabenold 1987). Seasonal roosts (Sweeney and Fraser 1986) and subroosts (Blanco and Tella 1999) are used annually during specific periods, and ephemeral roosts are used briefly to facilitate access to temporary foraging resources (Sweeney and Fraser 1986). Central roosts (Coleman and Fraser 1989), or primary roosts (Coleman and Fraser 1989) are used relatively frequently as birds move within a roost system (Rabenold 1987), which is defined as a series of adjacent communal roosts used by a local population (Rabenold 1987). Formation and dissolution of seasonal roosts appear to contribute to cycles observed at permanent roosts (Sweeney and Fraser 1986). Subroosts and seasonal roosts may offer access to more potential breeding sites than do main roosts (Blanco and Tella 1999), providing different functionality to different roost types. In the language of the Social Refuge–Territory Prospecting hypothesis proposed here, main roosts may serve primarily a social refuge function, and subroosts, which are called "pairing centers" by Blanco and Tella (1999), may serve primarily a territory prospecting function.

Future Research. A weakness in our work is that the communal roost data we present here is drawn from a single site. However, because no counts of caracaras at communal roosts had ever been conducted prior to our work, no other data were available for comparison. Future research should seek to evaluate elsewhere the patterns we observed at the communal roost we studied. Future research could also focus on exploring how recruitment and mortality occurs in caracaras by attempting long-term tracking of birds from their natal territories, through the nonbreeding and floater life stages, to breeding territories, and by evaluating the potential for inclusive fitness when doing so. If the Social Refuge–Territory Prospecting hypothesis is correct, then long-term tracking should indicate settlement in areas explored during previous breeding seasons, and mechanisms of mortality of nonbreeding individuals during the breeding season should indicate intraspecific conflict with breeding birds as a cause.

Another weakness in our study is the lack of inclusion of a formal mathematical model for the Social Refuge–Territory Prospecting hypothesis. Future research focused on evaluating our hypothesis with a multiple-competing-hypotheses framework may benefit from (1) creating and framing testing around a formal mathematical model, and (2) using that model to guide a more statistically elegant analysis of seasonal differences in count data at communal roosts.

Conservation Implications. Though communal roosting by caracaras has been known since the 1980s and 1990s (Lasley 1982, Johnson and Gilardi 1996), and continues to be reported (Dwyer 2010, Morrison and Dwyer 2012), our observations provide the first long-term record of year-round use. The conservation implications of such roost use are undeveloped for caracaras (Smith et al. 2017), but in general management strategies that omit nonbreeding individuals in species where floaters are present may fail to correctly identify why management goals are unmet (as they are in caracaras; USFWS 2008), and may consequently lead to ineffective or even counterproductive management actions (Penteriani et al. 2011).

If communal roosts function in the dispersal of caracaras as hypothesized here, then the current conservation efforts, which focus entirely on breeding sites, may be ineffective in the long term.

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Specifically, during the social refuge phase, loss of communal roosts could reduce survival of nonbreeding birds during nonbreeding seasons, and during the territory prospecting phase, loss of communal roosts could limit nonbreeder's ability to visit potential breeding territories. Together these negative impacts could reduce recruitment to the breeding population if existing breeding birds die and are not replaced. We don't know for certain how communal roosts function in the ecology of nonbreeding caracaras, but we do know that there are at least 13 communal roosts spaced regularly throughout the species' range (Dwyer 2010), that individual nonbreeding caracaras move regularly among these sites (Dwyer 2010), and that 10 of the 13 known communal roosts are within habitat identified as having high or very high probabilities of nesting caracaras (Smith et al. 2017).

Until managers better understand the role of communal roosts in the ecology of Florida's caracaras, management of this population should focus on protecting roosts along with nest sites. Future conservation-oriented research should examine additional communal roosts, compare communal roosting habitat to breeding habitat, and identify whether individuals move among communal roosts.

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