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NEST PROVISIONING AND SOCIALITY AT HARRIS'S HAWK NESTS IN SOUTH TEXAS

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ABSTRACT.—The Harris's Hawk (*Parabuteo unicinctus*), a social raptor species, often breeds and hunts cooperatively in groups typically consisting of a dominant breeding pair and one or more auxiliary group members. Why these birds form social groups is not completely understood, but one hypothesis is that the ability to hunt cooperatively may benefit groups with a higher hunting success rate or facilitate the capture of larger prey than an individual hawk could catch on its own. To test the hypothesis that group hunting affects patterns of prey delivery and the types of prey delivered to nests, we recorded videos of prey deliveries in May and June at nests of five breeding groups and five breeding pairs in Cameron County and Willacy County, Texas. In contrast to the diets of Harris's Hawks in New Mexico and Arizona that depend heavily on lagomorphs, we documented mostly avian prey items (39.1% of prey deliveries) and rodent prey items (39.1%), and only 0.7% lagomorphs ($n = 284$ prey items recorded). Significantly more prey items per day were delivered to nests with more nestlings. Importantly, and contrary to our hypothesis, pairs delivered more prey items per day on average than groups; this pattern was not significant, but this may be attributable in part to a small sample size of nests. These results suggest that the presence of auxiliaries may not necessarily provide direct benefits to offspring during the nest provisioning stage at late spring and summer nests in south Texas.

KEY WORDS: *Harris's Hawk*; *Parabuteo unicinctus*; *cooperative breeding*; *diet*; *nest provisioning*; *social behavior*.

APROVISIONAMIENTO DEL NIDO Y SOCIABILIDAD EN NIDOS DE *PARABUTEO UNICINCTUS* EN EL SUR DE TEXAS

RESUMEN.—*Parabuteo unicinctus* es un ave de presa sociable, que a menudo se reproduce y caza de manera cooperativa en grupos que generalmente consisten en una pareja reproductora dominante y uno o más miembros del grupo auxiliar. No se comprende completamente por qué estas aves forman grupos sociales,

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pero una hipótesis es que la capacidad de cazar de manera cooperativa puede brindarles a los grupos el beneficio de una tasa de éxito de caza más alta o bien facilitar la captura de presas más grandes que las que un solo ejemplar podría atrapar por sí solo. Para evaluar la hipótesis de que la caza grupal afecta los patrones de aporte de presas y los tipos de presas aportadas a los nidos, grabamos vídeos de aportes de presas en mayo y junio en nidos de cinco grupos reproductores y cinco parejas reproductoras en los condados de Cameron y Willacy, Texas. A diferencia de la dieta de *Parabuteo unicinctus* en Nuevo México y Arizona, que depende en gran medida de lagomorfos, documentamos principalmente aves (39.1% de las entregas de presas) y roedores (39.1%) como las presas aportadas en mayor número, con solo un 0.7% de lagomorfos ($n = 284$ presas registradas). Se aportaron significativamente más presas por día a los nidos con más polluelos. Es importante destacar que, contrariamente a nuestra hipótesis, las parejas aportaron más presas por día en promedio que los grupos, siendo este patrón no significativo, pero esto puede atribuirse en parte a un tamaño muestral de nidos pequeño. Estos resultados sugieren que la presencia de individuos auxiliares no necesariamente proporciona beneficios directos a la descendencia durante la etapa de aprovisionamiento del nido para los nidos de finales de primavera y de verano en el sur de Texas.

[Traducción del equipo editorial]

INTRODUCTION

Cooperative breeding, in which more than a pair of individuals assist in raising a single brood, occurs regularly in about 9% of all bird species and 6% of species in the family Accipitridae (Cockburn 2006). In some cases, cooperation may allow individuals to survive in difficult environmental conditions, and several studies have suggested that the evolution of cooperation is favored in harsh or highly variable environments when environmental conditions and food resources are unpredictable across seasons or years (e.g., Rubenstein and Lovette 2007, Jetz and Rubenstein 2011, Koenig and Walters 2015, Koenig 2017). One way for animals to cope with an uncertain or challenging food source is to develop social foraging strategies such as cooperative hunting (Bednarz 1988b).

For some carnivores, cooperative (or “group”) hunting, in which more than two individuals actively pursue prey together, may be one major advantage of living in social groups (Schoener 1971). Group hunting could, for example, increase overall hunting success, as seen in lions (*Panthera leo*), which rely on cooperative hunts especially during the dry season, and which experience higher hunting success as group size increases (Packer and Rutan 1988, Stander 1991). Group hunting could also facilitate the acquisition of prey larger than that which could be caught by a single individual, as seen in some cooperative carnivores like African wild dogs (*Lycan pictus*; Creel and Creel 1995).

Although cooperative hunting by birds has been less thoroughly studied than cooperative hunting in mammals, species such as the Golden Eagle (*Aquila chrysaetos*), Aplomado Falcon (*Falco femoralis*), Lanier Falcon (*Falco biarmicus*), and Peregrine Falcon

(*Falco peregrinus*) are known to hunt cooperatively in pairs (Ellis et al. 1993). In these species, hunting in pairs (or “tandem hunting”) may assist with the opportunistic capture of challenging prey and may help predators cope with hunting in complex habitats or harsh environmental conditions (Ellis et al. 1993, Kimball et al. 2003). For Peregrine Falcons, tandem hunts are 14.5% more successful than solo hunts by female falcons (Thiollay 1988), and for Aplomado Falcons, tandem hunts are 25% more successful than solo hunts (Hector 1986). Evidence of cooperative hunting among larger, stable social groups has been observed in certain raptor species known to breed cooperatively, such as the Variable Hawk (*Geranoaetus polyosoma*), Pale Chanting-Goshawk (*Melierax canorus*), and Harris’s Hawk (*Parabuteo unicinctus*; Bednarz 1988b, Malan 1998, Orellana and Figueroa Rojas 2005).

The Harris’s Hawk is native to desert and savannah habitats of North and South America, with a northernmost range extending into southern Arizona, New Mexico, and Texas. In North America, Harris’s Hawks often live and breed cooperatively in groups consisting of a single breeding pair and one or more auxiliary group members (or “helpers”). These auxiliaries are often male offspring from previous broods that remain on their parents’ territory for up to 3 yr (Bednarz 1987, Dawson and Mannan 1991).

Groups of Harris’s Hawks typically remain together year-round and will sometimes engage in sophisticated cooperative hunts to pursue prey, particularly lagomorphs, which make up a significant portion of their diet in Arizona and New Mexico (Bednarz 1988b). During the winter, overall hunting success and individual food intake per group member

increase as group size increases (Bednarz 1988b). In Arizona, auxiliaries in a breeding group of Harris's Hawks assist with provisioning the breeding pair's nestlings through both solo and cooperative hunts. For birds breeding in groups, the majority of hunts are cooperative rather than solo (Dawson and Mannan 1991), suggesting that group hunting may play an important role in provisioning offspring as well as sustaining adult group members. Although nests attended by pairs and groups do not differ in the number of nestlings successfully raised to fledging, groups are more likely to attempt to raise a second annual clutch, and offspring raised by groups are on average larger in mass at the time of fledging than offspring from nests attended only by the breeding pair (Bednarz 1987). Studies of other bird species suggest that nestlings with greater mass at fledging tend to survive longer (e.g., Both et al. 1999, Monrós et al. 2002), though this remains unstudied in Harris's Hawks.

One hypothesized benefit of group hunting in this species, in addition to increasing the overall success rate during hunts, is allowing hawks to subdue larger prey animals than would otherwise be able to be taken by birds hunting alone or in pairs (Bednarz 1988a, 1988b). Another related hypothesis is that Harris's Hawks that hunt in groups have higher hunting success in denser or otherwise more challenging habitat (Coulson and Coulson 2013), suggesting that hawks hunting in groups may be able to exploit different prey than hawks that hunt alone.

In this study we focus on nest provisioning to test the hypothesis that the presence of auxiliary group members affects patterns of prey delivery and the types of prey delivered to nests during the late spring and summer. Specifically, we (1) compare the daily number of prey deliveries between the nests of groups and pairs, and (2) compare the proportion of different prey types delivered to nests tended by pairs or groups. We predicted that nests tended by groups would receive more prey deliveries per day and a greater proportion of larger prey items (e.g., lagomorphs) than nests tended by pairs. Such results would support the hypothesis that the presence of auxiliaries, and by extension group hunting, provides a foraging advantage over solo hunting.

METHODS

Study Area and Species. From May to June in 2018 and 2019, we monitored active Harris's Hawk nests in Cameron and Willacy Counties, Texas, USA (26.1384°N, 97.6298°W). Clark (2017) documented

that 56% of the species' breeding territories in this area are occupied by groups with three or more individuals; the rest are occupied by pairs. In south Texas, Harris's Hawks are residents of thornscrub forest and savannah habitat, but have also established themselves in agricultural and residential areas in the Brownsville-Harlingen Metropolitan Area. We primarily searched for active Harris's Hawk nests (with eggs or young) in Laguna Atascosa National Wildlife Refuge and the Lower Rio Grande National Wildlife Refuge, and we opportunistically monitored nests that we located or that were reported to us outside of wildlife refuges as well. Many of the Harris's Hawks in this study population were color-banded with a unique and visible two-digit code to assist with individual identification.

We began nest searching in mid-March and continued through June. We searched for active nests from roadsides, scanning from a car with spotting scopes. In any area where we sighted Harris's Hawks, we observed the birds for signs of breeding activity, such as frequent alarm calling, copulation, gathering nesting material, or carrying prey. If we could not locate a nest from the road, we searched the vicinity of hawk activity on foot with landowner permission.

In south Texas, Harris's Hawks nest in a diversity of tree species (and sometimes human-made platforms) of varying heights, ranging from approximately 2 m high in yucca trees (*Yucca treculeana*) to greater than 11 m high in taller tree species. Harris's Hawks lay 1–5 eggs, with a typical clutch size ranging from 2 to 4 eggs (Dwyer and Bednarz 2020), and the eggs hatch asynchronously (Bednarz and Hayden 1991). The nestlings are regularly shaded by an adult during daylight hours until they are 1 wk old, at which point the adults greatly reduce shading behavior (Mader 1979). Shading behavior continues to decline as the nestlings age. Nestlings may begin self-feeding as early as 18–20 d of age (Dwyer and Bednarz 2020), and begin leaving the nest after 40 d of age, with males fledging at an average of 44.8 d, and females fledging at an average of 47.9 d (Bednarz and Hayden 1991).

Video Monitoring. We modeled our camera systems on those designed by Cox et al. (2012). We used Supercircuits WL-TC20B security cameras to video record prey deliveries. We set these cameras to motion detection and painted all cameras brown for camouflage. We typically mounted cameras with zip-ties to a sturdy branch either above or beside the nest cup, and angled the camera to view as much of the

nest cup as possible. In most cases, the camera sat ≤ 1 m away from the nest. At nests in yuccas where the camera could not be mounted directly to the trunk of a tree, we mounted the camera to an adjacent PVC pole that had been painted brown and affixed to a yucca panicle. We used a 20-m Bayonet Neill-Concelman cable to connect each security camera to a Supercircuits MDVR25HR miniature digital video recorder (micro DVR), which recorded to a 32 GB SD memory card. A 12V 35Ah deep-cycle marine battery powered each camera. We placed each micro DVR in a small plastic container on the ground next to the deep-cycle battery for easy access and protection from the elements. We banded nestlings and installed cameras at nests where the age of the youngest nestling at the time of installation ranged from 19 to 34 d old. We visited each video-monitored nest every 3 d to change batteries and memory cards, and maintained cameras at nests until the last nestling fledged. In 2018, we collected prey delivery data between 1 June and 28 June. In 2019, we collected prey delivery data between 14 May and 20 June.

We analyzed footage from 10 video-recorded nests: 4 nests in 2018 and 6 nests in 2019. Of these 10 nests, 5 were group nests and 5 were pair nests. We did not include data from any of the same nest locations, breeding territories, or marked birds in both 2018 and 2019. We determined breeding unit type (group versus pair) through 5 cumulative hr of observation at each nest territory following the protocol of Clark (2017). A nest was counted as a “pair” nest if only two unique hawks were seen in the nesting area at any point during the observation period, and a nest was counted as a “group” nest if at least three unique hawks were seen in the nesting area. Because Dawson and Mannan (1989) recommend a minimum of 10 hr of observation to confidently determine the exact group size for breeding Harris’s Hawks, we decided to classify breeding units as either groups or pairs to account for the possibility of underestimating the exact number of hawks in each group. We also supplemented the observation data by counting the number of hawks observed in the vicinity of the nest each time we changed camera batteries and memory cards, and reviewed all nest video data for attendance of any auxiliaries, which confirmed the initial breeding unit types assigned through focal nest-territory observations. If banded, individual nest attendants were identified by their unique color bands, but even unbanded hawks could typically be identified by unique facial characteristics

as well as identifiable plumage and molt patterns. For example, some individuals could be distinguished by clear variation in tail molt or heavy body molt, or by the prominence of the bare part of the supraorbital ridge, as compared to other unbanded individuals in the group.

Prey Item Identification. We identified all prey items delivered to nests between 0600 and 2100 H (CST) on each day when the camera was fully functional with prey items visible the entire day (not interrupted by camera system malfunction, significant obstruction of camera view, or a full memory card), and only for days when the total number of prey deliveries could be accurately counted. In some cases, we could view only parts of prey items on camera. In these cases, we identified items if clearly identifiable characteristics such as limbs or a tail were visible. If a prey item was badly dismembered or mostly out of sight on camera and could not be identified at all, we classified it as “unknown” (16.9% of overall prey deliveries). For analysis, we classified prey items by taxonomic class or order: rodent (order Rodentia), lagomorph (order Lagomorpha), bird (class Aves), or amphibian/reptile (classes Amphibia and Reptilia). Only one prey item (a possible nine-banded armadillo [*Dasybus novemcinctus*]) fell into a different taxonomic group than those listed.

Statistical Analyses. All statistical analyses were performed with the software R version 3.6.1 (R Core Team 2019), using generalized linear mixed-effect models (GLMMs) in the *glmmTMB* package (Brooks et al. 2017), with a Conway-Maxwell Poisson distribution. We constructed three models to test whether (1) total daily prey deliveries, (2) total daily rodent deliveries, and (3) total daily bird deliveries were correlated with breeding unit type (group nest or pair nest). Explanatory variables were breeding unit type (group or pair), year, nestling age (age of the oldest nestling), brood size, daily total precipitation, and percent urbanization, with nest ID as a random effects variable. We included data from 58 total days of nest video (approximately 870 total video-recorded hours) in the final models.

Urbanization was calculated as a percent area within a 977-m radius buffer around each nest that fell under the National Land Cover Database (NLCD) definition of “developed land” (ranging from open developed land to high-intensity developed land, NLCD categories 21, 22, 23, and 24; https://www.usgs.gov/centers/eros/science/national-land-cover-database?qt-science_center_

Table 1. Minimum and maximum numbers of daily prey deliveries for each video-recorded Harris's Hawk nest.

NEST ID	BREEDING UNIT TYPE	BROOD SIZE	TOTAL NUMBER OF DAYS OF OBSERVATION	NUMBER OF PREY DELIVERIES PER DAY (MINIMUM–MAXIMUM)		
				BIRDS	RODENTS	TOTAL
18-Cemetery	Group	2	9	1–9	0–1	2–10
18-Massey	Group	1	8	0–1	0–5	1–5
18-Kingston	Group	1	2	0	3–4	3–5
19-CR1400	Group	4	4	3–5	0	3–7
19-Quicksilver	Group	3	3	0	6	6–7
18-HW511	Pair	2	7	0–3	0–2	2–5
19-BulkPack	Pair	3	4	2–7	0–2	6–13
19-Fish	Pair	2	8	0–3	0–5	2–10
19-RioHondo	Pair	1	4	0–5	0–1	1–7
19-Williams	Pair	2	9	0–2	1–8	3–9

objects=0#qt-science_center_objects). We chose a 977-m buffer radius because a circle of this area approximates the known average home range size for Harris's Hawks (Dwyer and Bednarz 2020). We extracted land cover data for the year 2011 (the most recent data available). We included this variable to account for variation in habitat structure between nests in areas with different extents of land development. Although land cover proportions in 2011 may have differed somewhat from land cover proportions in 2018 and 2019, no video-recorded nests were located near areas of rapid recent development or other significant recent land use changes. In addition, all video-recorded nests and surrounding areas were visited in-person multiple times and land use appeared consistent with the extracted urbanization data for each territory.

We extracted daily local precipitation totals for each day of analysis from the Global Historical Climatology Network data compiled by the National Oceanic and Atmospheric Administration (Weather Station ID#: US1TXCMR090, Brownsville, Texas, 25.929928°N, 97.505535°W, located within 57 km of all nests; Menne et al. 2012). We included this variable because we observed that on days of heavy rainfall the adults hunted less actively.

Ethical Note. This study was conducted with Institutional Animal Care and Use Committee (IACUC) approval from the University of North Texas (UNT IACUC protocol 18-012) and with the approval of all relevant property owners and wildlife refuge authorities. We chose which nests to video record based on nest accessibility and the ability to maintain each nest camera with minimal disturbance to the attending adults. At all but one nest, we

installed video cameras at the same time that we banded the nestlings to minimize the number and duration of disturbances to each nest. At one nest, we installed the video camera 3 d after banding the nestlings due to equipment malfunctions on the planned date of install. However, this camera installation took less than 30 min and the attending adult hawks resumed normal activity by the following morning.

To avoid the risk of nestlings overheating from a lack of parental shading, we installed cameras when the nestlings were old enough to self-thermoregulate even at the hottest time of day. We also reviewed nest camera footage the day after camera installation to make certain that the adults had resumed visiting the nest and delivering prey to the nestlings. In all cases, the adults had resumed nest attendance and prey deliveries by the day after camera installation. Additionally, none of the installed cameras obstructed nestlings or adults from moving, standing, or feeding normally on the nest. We changed batteries and memory cards at nests as quickly and as infrequently as possible to minimize disturbance (<10 min per visit), and we only removed cameras from nests when we were certain all nestlings had safely fledged.

RESULTS

We documented 284 prey deliveries across all 10 nests included in this study. Overall proportions of prey deliveries across all nests were as follows: birds (39.1%), rodents (39.1%), reptiles and amphibians (3.9%), lagomorphs (0.7%), unknown (16.9%), and other (0.3%; Tables 1, 2).

Table 2. List of prey (to most specific possible taxa) documented at video-recorded Harris’s Hawk nests.

CLASS	ORDER	FAMILY	GENUS/SPECIES	
Amphibia	Anura	Bufo		
Mammalia	Rodentia	Sciuridae	<i>Xerospermophilus spilosoma</i>	
		Cricetidae	<i>Sigmodon</i> sp.	
			<i>Neotoma micropus</i>	
	Lagomorpha	Leporidae	<i>Sylvilagus</i> sp.	
	Cingulata	Dasyopodidae	<i>Dasyopus novemcinctus</i> ^a	
Reptilia	Squamata	Teiidae	<i>Aspidoscelis</i> sp.	
		Phrynosomatidae	<i>Sceloporus olivaceus</i>	
Aves	Galliformes	Cracidae	<i>Ortalis vetula</i>	
	Columbiformes	Columbidae	<i>Zenaida</i> sp.	
	Passeriformes	Icteridae	<i>Quiscalus mexicanus</i>	
			Mimidae	<i>Mimus polyglottos</i>

^a Suspected but not confirmed identity.

Pairs tended to deliver more total prey items per day, on average, than did groups, but this pattern was not statistically significant ($Z = 1.765$, $df = 48$, $P = 0.078$; Supplemental Material Table S1 includes detailed model results). The number of daily rodent deliveries did not differ between groups and pairs ($Z = -0.317$, $df = 48$, $P = 0.752$), nor did the number of daily bird deliveries ($Z = 1.284$, $df = 48$, $P = 0.199$; Fig. 1).

The number of total daily prey deliveries was related to brood size: nests with more nestlings

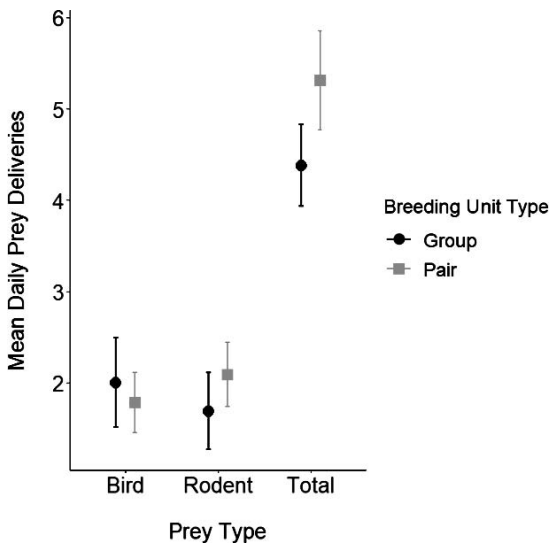


Figure 1. Mean daily prey deliveries to Harris’s Hawk nests as a function of prey type (bird, rodent, and total) for two breeding unit types. Figure reports raw means and standard errors. Sample sizes: group ($n = 5$ nests), pair ($n = 5$).

received more birds per day ($Z = 2.220$, $df = 48$, $P = 0.026$) and more total daily prey deliveries ($Z = 2.487$, $df = 48$, $P = 0.013$; Fig. 2). The daily number of rodents delivered to a nest, however, was not related to brood size ($Z = -1.384$, $df = 48$, $P = 0.166$).

The number of total daily prey deliveries did not differ between 2018 and 2019 ($Z = 0.377$, $df = 48$, $P = 0.706$), nor did the number of daily bird deliveries ($Z = -1.148$, $df = 48$, $P = 0.251$) or daily rodent

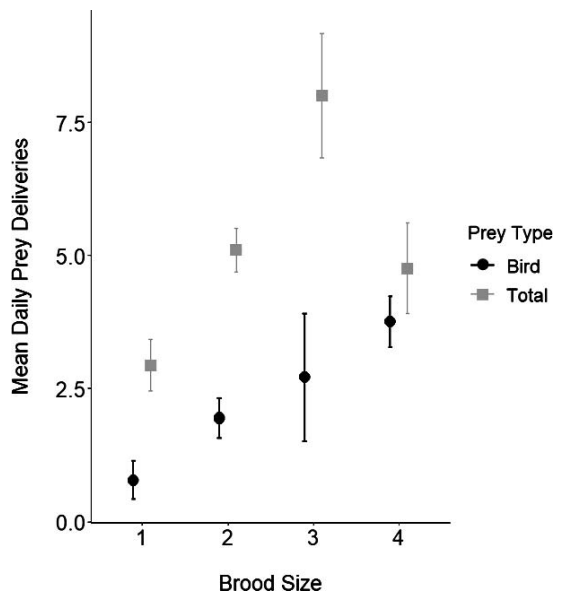


Figure 2. Mean daily prey deliveries to Harris’s Hawk nests as a function of brood size (1–4 nestlings) for two prey types (bird and total). Figure reports raw means and standard errors. Sample sizes: 1 nestling ($n = 3$ nests), 2 nestlings ($n = 4$), 3 nestlings ($n = 2$), and 4 nestlings ($n = 1$).

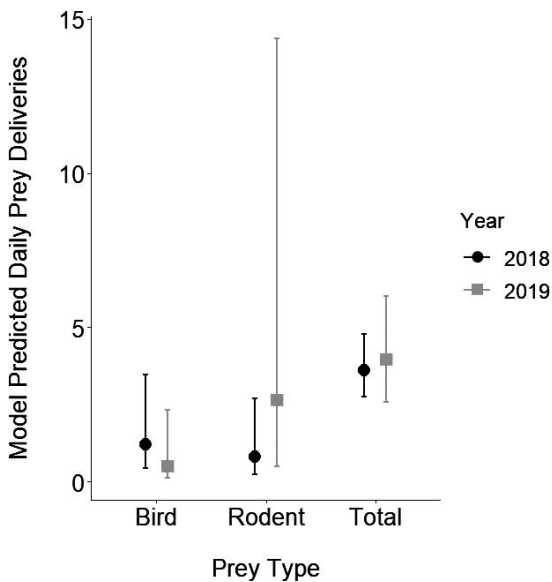


Figure 3. Model predicted daily prey deliveries as a function of prey type (bird, rodent, and total) during two years (2018 and 2019). Figure reports model predicted values and 95% confidence intervals. Sample sizes: 2018 ($n = 4$ nests), 2019 ($n = 6$).

deliveries ($Z = 1.312$, $df = 48$, $P = 0.190$; Fig. 3). Also, the number of total daily prey deliveries was not correlated with nestling age ($Z = 0.101$, $df = 48$, $P = 0.919$), nor was the number of daily bird deliveries ($Z = 0.551$, $df = 48$, $P = 0.582$) or daily rodent deliveries ($Z = -0.783$, $df = 48$, $P = 0.433$). In addition, the number of total daily prey deliveries was not correlated with urbanization ($Z = -0.871$, $df = 48$, $P = 0.384$), nor was the number of daily bird deliveries ($Z = 0.323$, $df = 48$, $P = 0.747$) or daily rodent deliveries ($Z = -0.552$, $df = 48$, $P = 0.581$). Further, the number of total daily prey deliveries was not correlated with daily total precipitation ($Z = 1.726$, $df = 48$, $P = 0.084$), nor was the number of daily bird deliveries ($Z = -0.871$, $df = 48$, $P = 0.384$) or daily rodent deliveries ($Z = 0.554$, $df = 48$, $P = 0.579$).

DISCUSSION

The results of this study are limited by a small sample size of nests, but contrary to our predictions, pairs delivered, on average, nearly one more prey item to their nests per day than groups. Although this difference was not statistically significant, it could suggest that groups do not gain a foraging advantage over pairs during the late spring and summer breeding season. Compared to Arizona

where auxiliary group members have been observed playing an active role in procuring prey for nestlings (Dawson and Mannan 1991), it is possible that auxiliaries in south Texas may not contribute much to provisioning nestlings, or that the benefits of cooperating are indirect. In south Texas, Clark (2017) observed auxiliaries together with their groups more often after the nestlings had fledged, suggesting that auxiliaries could play a more active role in provisioning the nestlings after they have left the nest. Additionally, because Harris's Hawks breed all year in this area, auxiliaries may play a larger role during nesting attempts outside of the late spring and summer. Notably, despite groups delivering fewer prey items per day than pairs, all nestlings fledged successfully at the video-recorded nests, suggesting that groups were still able to meet the food demands of their nestlings at least through fledging despite delivering fewer prey items per day on average. In south Texas, groups fledge an average of 2.1 nestlings per nest, and pairs fledge an average of 2.0 nestlings per nest (Gibbons 2021), suggesting that groups are not necessarily more likely to raise larger broods or fledge more young per nesting attempt.

Ecological variables might also explain differences in prey delivery frequency between groups and pairs. According to a hypothesis for cooperative breeding proposed by Gowaty (1981), cooperation may allow groups to breed more successfully than pairs in lower-quality habitat. For Harris's Hawks, if the benefits of cooperation (such as group hunting) allow groups to breed in areas with lower prey abundance, this could help explain why groups deliver fewer prey items per day to their nests than pairs. There is little support for this hypothesis in the New Mexico population of Harris's Hawks, where habitat composition was found to be similar between group and pair home ranges (Bednarz and Ligon 1988), but this hypothesis has yet to be evaluated in south Texas, where hawks occupy a wide range of savannah and thornscrub habitats as well as more developed habitats. Of all variables included in the models, brood size was the only significant predictor of prey delivery frequency. Hawks with larger brood sizes delivered more total prey items per day as well as more birds per day. Although our data suggest that nests with four nestlings receive fewer prey items per day than nests with three (Fig. 2), this may be explained by sample size, as we only sampled a single nest with a brood size of four. The general trend, an increase in prey deliveries with increasing brood size,

has been found in several other species of birds, including several raptors (e.g., Kennedy and Johnson 1986, Dijkstra et al. 1990, Olsen et al. 1998, Giovanni et al. 2007). Our results suggest that Harris's Hawks increase provisioning effort when they have more nestlings to feed.

Summed across all nests, birds and rodents made up the majority (78.2%) of overall prey deliveries. Group and pair nests did not differ significantly in the number of birds nor the number of rodents delivered daily. In contrast to populations in Arizona and New Mexico which rely in large part on lagomorph prey (Bednarz 1988a, Dwyer and Bednarz 2020), Harris's Hawks in south Texas appear to rely very little on lagomorphs, which made up only 0.7% of overall prey deliveries to nests. The fact that neither groups nor pairs delivered many lagomorphs to their nests does not support the hypothesis that cooperation is driven by the ability for group-hunting hawks to better capture large prey animals in south Texas.

Although we did not conduct standardized surveys for local prey abundance, we regularly observed cottontail rabbits (*Sylvilagus* sp.) while nest searching, and infrequently encountered black-tailed jackrabbits (*Lepus californicus*) as well, suggesting that these hawks have some access to lagomorphs. However, our data suggest that this population of hawks may preferentially hunt rodents and birds instead during late spring and summer nesting attempts. The thornscrub and savannah habitats of south Texas are structurally more complex than some of the desert habitats in Arizona and New Mexico, and we suggest that the more complex vegetation structure in large parts of the Harris's Hawk's range in south Texas may make it more difficult for hawks to capture lagomorphs successfully. Given that this study was limited to the late spring and summer breeding season, it is also possible that group hunting is simply less beneficial to hawks during the summer compared to other times of year. Harris's Hawks are known to hunt cooperatively more frequently in the winter than in the summer (Dwyer and Bednarz 2020), so perhaps cooperation and group hunting does not provide a strong advantage during the summer breeding season, but instead helps hawks cope with limited prey abundance during the winter.

Although Dawson and Mannan (1991) reported that most prey items delivered to group nests were captured via cooperative hunts rather than solo hunts, it is possible that cooperative hunting among

groups in south Texas during the summer is simply less common than in New Mexico or Arizona. If relatively small prey is more abundant or accessible to hawks in the south Texas population, especially during the summer, perhaps there may be less selective pressure for them to hunt cooperatively or to even pursue difficult prey such as lagomorphs.

Despite taking relatively small prey items such as birds and rodents, Harris's Hawks in this study population did sometimes hunt cooperatively. Group hunting in Texas has also been reported by other researchers (Coulson and Coulson 1995, Clark 2017). On multiple occasions, we observed groups of hawks hunting together along tree lines or at the edge of thornscrub forest, scanning for prey from close perches and flying together, with other group members taking higher perches while one hawk dropped out of sight to the ground, presumably to capture or flush out prey. We could not determine what quarry they were hunting in these cases because ground vegetation blocked our view. In 2019, we directly observed a cooperative hunt of a Texas spiny lizard (*Sceloporus olivaceus*), in which a pair of adult hawks ambushed a lizard from opposite sides of a power pole, with one hawk flushing the lizard towards the other hawk, which captured it. The same year, we also observed a possible cooperative hunt of avian prey, in which two Harris's Hawks in flight both attempted to capture medium-sized songbirds (grackles or blackbirds, family Icteridae) at the same time in a single moving flock.

The results of this study, like the results of prior studies on the breeding biology and social behavior of Harris's Hawks, suggest that the benefits of cooperation are not clear-cut and may be influenced by a complex array of factors. If cooperative breeding does not directly benefit nestlings during the late spring and summer breeding season, as this study suggests, then what might be the advantage of breeding cooperatively? One possibility is that even if nestlings do not benefit directly from the presence of auxiliaries, they could still benefit after fledging. Delaying dispersal to remain at the natal territory as an auxiliary may benefit a young hawk with opportunities to gain hunting experience and to share in kills made by more experienced group members (Bednarz and Ligon 1988, Dawson and Mannan 1991), which could possibly benefit the auxiliary's long-term survival. Harris's Hawks are also known to sometimes initiate second or third nesting attempts, raising multiple broods in a single year, and groups in New Mexico are more likely than pairs to re-nest (Bednarz

1987). Even if nestlings in a single breeding attempt did not benefit directly from cooperation (through increased provisioning), cooperative groups in Texas could be able to increase annual reproductive output if they are capable of re-nesting more often than pairs. Also, cooperation may not help hawks in wetter years, but it could afford groups an opportunity to breed in harsh, dry breeding seasons when pairs would be forced to forgo reproduction, as is the case with the cooperatively polyandrous Galapagos Hawk (*Buteo galapagoensis*; Faaborg 1986). In this way, cooperation may not always be the most advantageous strategy but could act as more of a safety net, possibly allowing groups to breed in harsher conditions or ecological crunch seasons (Emlen 1982).

Given that diet and patterns of nest provisioning appear to differ between Harris's Hawks in south Texas and those in Arizona and New Mexico, future studies in this population should focus on better characterizing the benefits of group-living and the role of auxiliaries when these hawks are not breeding. Directly studying the group hunting tactics of hawks in south Texas, especially during the winter, as Bednarz (1988b) did in New Mexico, would allow us to characterize the role of auxiliaries, and understand the prevalence and role of group hunting in this population. Further study of habitat selection between groups and pairs in south Texas could also allow us to determine whether groups appear better able to exploit more complex or challenging habitats, as proposed by Coulson and Coulson (2013). A longer-term study, especially including breeding data outside of the summer, could allow us to test whether the occurrence of cooperative breeding and the reproductive success of groups and pairs are correlated with large-scale environmental variables like annual rainfall and seasonal prey abundance. Importantly, the results of this study are based on a small sample size and thus limited in scope; future studies would greatly benefit from a larger sample size of nests. Through further study of the ecology and social behavior of Harris's Hawks in south Texas, researchers can work toward a better understanding of the selective forces favoring and maintaining social behavior in this cooperative species.

SUPPLEMENTAL MATERIAL (available online). Table S1: Full model results from the models examining the relationship between explanatory variables and the delivery of all prey items, only rodent prey, and only bird prey.

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