SHORT COMMUNICATIONS

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DEVELOPMENT OF HUNTING BEHAVIOR IN HACKED APLOMADO FALCONS

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The extent to which hunting is instinctive in young raptors as proposed by Brown and Amadon (1968) is difficult to investigate in wild populations. Parents of many species entice fledglings by carrying prey items, release or flush live prey in the vicinity of fledglings, and accompany them on hunting forays (Newton 1979, Schaadt and Rymon 1982, Sherrod 1983). However, numerous restoration projects involving the release ("hack") of young raptors into the wild, as developed centuries ago by falconers, have shown that hunting proficiency readily develops in the absence of parents (Sherrod 1983, Mutch et al. 2000). Moreover, hacked raptors may develop at rates similar to their wild counterparts; for example, hacked Peregrine Falcons (*Falco peregrinus*) and Red-necked Falcons (*Falco chicquera*) fledged and began killing prey at ages comparable to those in wild populations (Sherrod 1983, Bednarek 1993). The "hacking" procedure therefore facilitates the study of innate components involved in the ontogeny of hunting behavior.

The northern Aplomado Falcon (*Falco femoralis septentrionalis*) is particularly suited to such investigations as it is naturally tolerant of human presence and easily observed in its open savanna habitat, where it typically hunts from isolated perches. Of further interest is that adult pairs hunt cooperatively for avian prey, a mode that Hector (1986) believed an inherent tendency as based on his observations of breeding adults in eastern Mexico. In this report, we summarize our records and those of numerous observers who attended the development of hacked Aplomado Falcons released by The Peregrine Fund in Texas since 1993. Herein, we describe the development of their hunting behavior in the absence of parental influence.

METHODS

Study Area. Falcons were released in Texas (N = 25 release sites) at three focal areas: the lower Rio Grande valley in the vicinity of Laguna Atascosa National Wildlife Refuge (NWR); the coastal bend of southeastern Texas, including Aransas NWR and Matagorda Island NWR; and western Texas in Jeff Davis County. Vegetation at sites included savanna, coastal prairie, and Chihuahuan grassland/desertscrub (see McAlister and McAlister 1995, Perez et al. 1996, Powell 2000).

Methods. Procedures for the release of Aplomado Falcons were modified from those developed for Peregrine Falcons (Sherrod et al. 1987, Mutch et al. 2000). Following a pilot study in 1986–89, large-scale releases of Aplomado Falcons began in 1993 and continued through 2002, with 354 female falcons and 443 male falcons released during that period. At about 30 d of age, young falcons were transported to release sites in Texas; these featured 3–5 m tall towers, each topped with a release box facing away from an observation blind. Release groups of 2–8 falcons were placed within similar-aged cohorts regardless of gender. While still in release boxes, the falcons were fed and monitored by attendants. Boxes were opened when falcons were 38–41 d old, and the attendants continued to provide food and monitor the site daily for 6 wk following release. All falcons were banded with Geological Survey bands and anodized aluminum color bands with 1–2 alphanumeric characters, allowing attendants to identify individuals from a distance. Falcons were continuously observed during daylight hours for the first 3 d following a release, and then during morning and evening hours only (dawn to 1100 H and 1500 H to dusk). Following the close of a release site, attendants provided reports summarizing the releases, dispersal, hunting behaviors, and unusual events observed at that site.

We extracted data from 46 project reports from 1993–2002 representing 22 release sites. Hunts were classified to mode as either solitary or group, with all hunts involving two or more falcons termed "group hunts," regardless of notes suggesting the hunts could be considered group, pseudocooperative, or cooperative (Ellis et al. 1993). Kills were recorded when a hunt ended successfully, or circumstantially determined when a falcon was seen with prey other than that supplied at the hack tower. We recorded 305 separate hunts, including 30 putative (circumstantial) kills, or 6.6 (95% Confidence Interval = ±1.8, range 1–26) per site/yr.

Statistical Analyses. We pooled data from west and south Texas, as separate analyses showed similar mean values and widely overlapping 95% confidence intervals (for age at first pursuit; female in south Texas, N = 65, $\bar{x}$ age = 63.9 d, 95% CI = ±3.1; female in west Texas, N = 11, $\bar{x}$ age = 65.7 d, 95% CI = ±7.9; males in south

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Table 1. Comparison by gender of first vertebrate pursuits and vertebrate kills in hacked Aplomado Falcons. Values are means in days (95% confidence intervals).

	FEMALE			MALES		
	$\bar{x}$		N	$\bar{x}$		N
First pursuits						
Age	64.1	(61.4–66.9)	76	59.1	(56.2–62.0)	78
Days since release	24.3	(21.5–27.0)	76	18.5	(15.5–21.4)	78
First kills						
Age	73.1	(67.1–79.0)	19	74.8	(69.3–80.4)	19
Days since release	32.4	(26.5–38.4)	19	34.8	(29.4–40.2)	19

Texas, $N = 69$, $\bar{x}$ age = 58.1 d, 95% CI = ±2.8; males in west Texas, $N = 9$, $\bar{x}$ age = 66.8 d, 95% CI = ±14.3). Our assumption that the behavior of each falcon was independent of its release cohort was supported by *F*-tests which showed that inter-cohort behavior was as variable as intra-cohort behavior (for age at first vertebrate pursuit: females, $F = 0.81$, df = 52, $P = 0.22$; males, $F = 0.91$, df = 47, $P = 0.37$). We compared differences between behaviors exhibited by male and female Aplomado Falcons, age differences at first solitary and first group pursuit of vertebrate prey by each individual, and temporal distribution and relative success of hunting modes. Data are expressed as means and 95% confidence intervals (95% CI) unless otherwise stated.

RESULTS AND DISCUSSION

Pursuit and Capture of Invertebrates. All sites reported hacked falcons chasing, capturing, and consuming insects from soon after release through the end of the observation periods (42 d after release). Pursuit of insects was so common that many attendants summarized rather than detailed specific hunts. Falcons caught insects in the air, plucked them from branches and grass stems, and pursued them by running on the ground. Groups of falcons chased the same insect, and falcons occasionally pirated insect prey from each other. At two sites, falcons gathered along the margins of controlled-burn plots and chased insects flushed from cover by the flames. Along the Texas gulf coast, falcons caught and consumed sand fiddler crabs (*Uca panacea*) locally abundant on tidal flats and in marshy areas (McAlister and McAlister 1995).

Pursuit of Vertebrates. Falcons pursued 67 species of vertebrates as apparent hunting targets, and 34 species during territorial defense or other aggression, the latter easily differentiated by the falcons' loud "kekking" vocalization (Keddy-Hector 2000). Raptors and large mammals evoked defensive behavior most frequently, but falcons also attempted to drive away an armadillo (*Dasypus novemcinctus*) and a Texas tortoise (*Gopherus berlandieri*).

All 275 vertebrate hunting attempts were directed towards birds, but two mammals and four reptiles were observed amongst the putative kills. Falcons typically flew directly from a perch toward prey in trees, on the ground, or flying past. The two largest species pursued with apparent hunting intent were Great Blue Heron (*Ardea herodias*: males 2576 g, $N = 17$; females 2204 g, $N = 15$) and Roseate Spoonbill (*Ajaia ajaja*: males 1240–1750 g, females 1400–1700 g; no sample size reported), and the smallest was the Ruby-throated Hummingbird (*Archilochus colubris*: males 3.0 g, $N = 202$; females 3.3 g, $N = 489$). The largest reported kill by the hacked falcons was a Mourning Dove (*Zenaida macroura*: males 123 g, $N = 140$; females 115 g, $N = 95$; Dunning 1993).

Sex Differences. Attendants recorded the first known vertebrate hunts for 154 individual falcons. Males pursued vertebrates earlier than females, measured both in age and d since release (Table 1). Kills were witnessed in 35 first successful vertebrate hunts, and an additional 30 putative kills were determined circumstantially. Of 38 first kills by known falcons, 19 were by females and 19 by males. Ages and d since release were similar for these falcons (Table 1).

Our data on the onset of vertebrate pursuit behavior agree with other studies of falcon development: the sexes of hacked Aplomado Falcons developed at different rates. Sherrod (1983) found that hacked male Peregrine Falcons began their first pursuits of vertebrates at an earlier age than females (50.6 d versus 55.7 d, $N = 43$ and 41, respectively). However, if we assume that the putative kill component represented prey killed by the possessor, male and female Aplomado Falcons appeared to kill vertebrate prey at the same age (Table 1). More putative kills were ascribed to females than males (15 to females, 7 to males). Although this could represent piracy by larger females upon smaller males, observations suggest that the tendency is rare (2 successful piracies and 5 piracy attempts in 275 hunts).

In any case, once Aplomado Falcons began pursuing vertebrate prey, females progressed to prey acquisition more quickly than males. On average, females obtained prey about 10 d after the onset of pursuit behavior, compared to males at 15 d. Bednarek (1993) also reported first kills at ca. the same age for each sex of hacked Rednecked Falcons; 60 and 68 d for males ($N = 2$) and 63

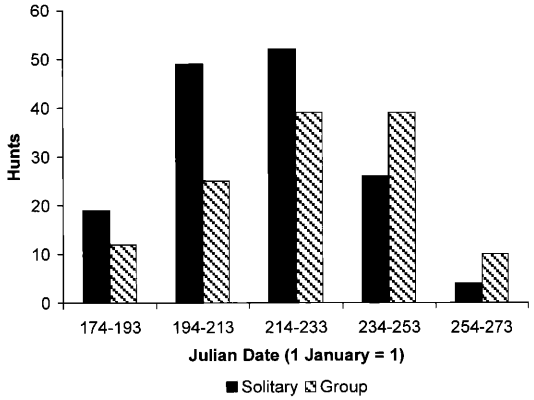

Figure 1. Incidence of solitary and group hunting by hacked Aplomado Falcons in Texas. Y-axis values are numbers of solitary and group hunts observed within 20-d intervals corresponding to first and last hunts observed (23 June–28 September 1993–2002).

and 69 d for females ($N = 2$). These results run counter to the often-held assumption that female raptors lag behind males in post-fledging development. Sherrod (1983) reported only a slight difference in the mean age of kills for peregrines (73.3 d for males and 76.8 d for females, $N = 62$ and 33, respectively).

Group Hunting. Of 275 pursuits of vertebrates reported as hunts, 125 involved more than one falcon (range 2–12 falcons) simultaneously chasing the same prey. Censoring hunts with group size reported merely as "group" ($N = 9$), 399 falcons participated in group hunts or 3.4 (95% CI = ±0.3) participants per hunt. Of hunts with known outcomes, 20 of 122 (16%) group hunts were successful, whereas 15 of 150 (10%) solitary hunts succeeded As the hacking periods progressed, group hunts were observed more often, and fewer solitary hunts were seen (Fig. 1). For the 23 falcons confirmed hunting both alone and in groups, there was no difference between the ages at first pursuit for either hunting mode (solitary = 59.4 d, 95% CI = ±5.3; group = 60.3 d, 95% CI = ±5 7). The increase in group hunts may therefore relate to factors other than the age of participants. It is quite possible that the prey base composition changed through the yr, with proportionally more recently-fledged, vulnerable passerines present in late summer. Moreover, the number of falcons per hack site increased throughout the season; at most sites, cohorts of falcons released sequentially throughout the hack season accumulated to a maximum of six cohorts per site, potentially presenting greater opportunities to participate in group hunts.

Group hunting commonly occurred at all hack sites. Although many group hunts were doubtless the consequence of several falcons coincidentally pursuing the same prey, detailed reports of group hunts suggested that some contained elements of cooperation. Ellis et al. (1993) suggested that true cooperative hunts, as described for mated pairs, family groups, and sibling groups, would have certain characteristics. These included coordinated movements, sometimes with some members performing rushing attacks having a low probability of capture success in order to increase the group's chance of capture; social signals such as vocalizations to initiate or coordinate the hunt; and orderly prey sharing. Observations of the hacked falcons were sometimes consistent with these criteria (Appendix, observations 1–3).

Group hunting was not limited to cohorts of hacked falcon nest mates. Hack sites were regularly visited by falcons released at other sites, especially those closely spaced within Laguna Atascosa and Matagorda Island NWRs. These visitors were accepted with little hesitation by the local falcons, and would feed from the same tower and join in group hunts. In later years, juvenile falcons dispersing from wild nests, always a month or more older than the hacked falcons, appeared at hack sites, and were similarly tolerated (Appendix, observation 4). Territorial adult falcons, whether previously hacked or wild-produced, displayed aggression toward hacked falcons, but other adults interacted benignly with the juveniles (Appendix, observation 5).

Hector (1986) found that adult Aplomado Falcons were significantly more successful when hunting birds as pairs than when alone: 45% of pair attacks were successful versus 21% of solo hunts. Success rates calculated for our data favored group hunts as well (16% versus 10%). Even so, from the standpoint of prey acquisition by individual hacked Aplomado Falcons, group hunts were far less efficient than solitary hunts. For group hunts in which both group size and hunt outcome were known, 386 falcons participated in 113 group hunts of which 20 were successful, leading to a success rate of 5% per participant, less than one half the frequency of success recorded for solitary hunts (10%). Because group hunting by recently fledged falcons is likely precursory to the cooperative hunting of adult pairs and because food is not usually shared among juveniles participating in group hunts, adaptive payoffs of this behavior would appear to be delayed a yr or more.

Our findings support those of other studies that young raptors quickly acquire foraging skills in the absence of parental influence. However, the young hacked Aplomado Falcons behaved differently than Peregrine Falcons: groups of hacked peregrines rarely share food and their conspecific interactions are markedly more aggressive (B. Mutch pers. comm.). Instead, our data support those of Hector (1986), who theorized that cooperative hunting is innate in Aplomado Falcons. He noted that throughout the species' range mated pairs hunt together yr-round, both sexes vocalize to instigate participation by their mates in hunting and defense activities, different pairs show the same division of labor in hunts, and nestlings and fledglings are more passive toward one another than those of other falcon species. The behavior ob-

served among the hacked Aplomado Falcons was similar to that of foraging adult pairs. Young Aplomado Falcons persisted in group hunt participation despite the lack of immediate payoff, which points to future benefits associated with the early practice of such behavior.

RESUMEN.—Examinamos 275 registros de comportamiento de caza, incluyendo 125 grupos de caza, entre polluelos de halcones perdiceros (*Falco femoralis*) en el sur de Texas. En promedio, los halcones machos comenzaron a perseguir presas vertebradas 5 días mas temprano que sus hembras "hermanas", sin embargo ambos sexos mataron presas vertebradas a la misma edad. Mientras que los grupos de caza estuvieron más propensos a ocurrir mas tarde en el año, los individuos de halcón perdicero no mostraron correlación entre la edad y la época cuando ellos participaron en la cacería cooperativa. Mas intentos de caza en grupo terminaron exitosamente (16% versus 10%); sin embargo, con una media de 3,4 participantes por grupo de caza, estos fueron mucho menos eficientes por participante (5% de oportunidades de éxito). Algunos grupos de caza mostraron características típicas de cacerías cooperativas exhibidas por las parejas de halcones perdiceros. Nuestras observaciones sugieren que los grupos de caza son innatos en los halcones Perdiceros y que las ineficientes cacerías en grupo de los jóvenes halcones pueden ayudar a desarrollar las habilidades sociales y las técnicas de caza necesarias para las futuras cacerías cooperativas con sus parejas.

[Traducción de César Márquez]

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APPENDIX—SELECTED OBSERVATIONS

1. A group of four falcons (64.8 ± 5.5 d old) chasing a Cliff Swallow (*Petrochelidon pyrrhonta*) surrounded it such that, as it tried to escape from one pursuing falcon, it met another in its path. Eventually the swallow sought refuge in a mesquite tree (*Prosopis glandulosa*) only to be flushed by one falcon as the others waited nearby and resumed the chase. Later, at least 10 falcons chased a pair of Loggerhead Shrikes (*Lanius ludovicianus*) in the same manner. The falcons gave short "chipping" vocalizations characteristic of those exhibited by mated pairs during cooperative hunts (Keddy-Hector 2000, Peregrine Fund unpubl. data) Both hunts were unsuccessful, but 8 d later three of the falcons (81 ± 1 d old) from the first hunt, caught a Cliff Swallow after chasing it high in the air. The successful falcon fed on his prey while the other two watched intently but passively.
2. Observers witnessed a successful hunt by five falcons on an Eastern Meadowlark (*Sturnella magna*). As it tried to escape across the open landscape, three falcons tail-chased, while two stooped from above. On the following d, a group of six falcons caught a small bird in the same manner. One month later, groups chased and killed Eastern Kingbirds (*Tyrannus tyran-*

nus). During one hunt, eight falcons chased a kingbird for about 1 min until it sought refuge in a mesquite. The falcons followed it, with five waiting in the treetop while three others ran and hopped through the lower branches until the kingbird flushed and was captured, a sequence often exhibited by mated pairs (Keddy-Hector 2000).

3. In 1993, a group of seven falcons chased and caught a Ladder-backed Woodpecker (*Picoides scalaris*). Several falcons fed on it simultaneously, while the others settled on perches nearby. When a Northern Harrier (*Circus cyaneus*) approached the kill site, two of the non-feeding falcons left the group and drove the harrier away while the others continued their meal undisturbed (C. Perez pers. comm.).
4. A wild hatch-year (HY) male falcon was found eating prey while perched on the rafters underneath one of the hack boxes. Attendants reported that this falcon "generously shared" his kill, possibly a swallow, with a female hacked falcon.
5. A wild-hatched adult female arrived at a hack site and led the first successful group hunt of the yr. She captured a meadowlark after chasing it together with two HY hacked falcons, all three stooping in turn. At a different hack site, a previously hacked adult female regularly visited from 1999–2002. This falcon occasionally fed from the tower, joined in hunts and tower defense, and tolerated food-begging from the HY falcons. Attendants described her behavior as "mentoring."

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SUMMER ROADSIDE RAPTOR SURVEYS IN THE WESTERN PAMPAS OF ARGENTINA

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Roadside surveys are useful for assessing habitat preferences of diurnal raptors. Although the limitations and biases inherent in roadside counts are well known (Fuller and Mosher 1987), roadside surveys serve as a practical means for rapidly assessing raptor distribution and abundance over large areas (Ellis et al. 1990). Roadside surveys have been used to compare species richness and abundance between broad regions and to assess impacts of anthropogenic-habitat transformations on raptors. These types of surveys have been carried out in Europe (Meyburg 1973), Africa (Cade 1969), North America (Woffinden and Murphy 1977), Latin America (Ellis et al 1990), Patagonia (Donázar et al. 1993), and a grassland-agricultural ecosystem in Argentina (Leveau and Leveau 2002). The distribution of raptors across central Argentina was surveyed east to west from Buenos Aires to Zapala, Neuquén (Travaini et al. 1995); we add to this body of knowledge and report results obtained from roadside raptor surveys carried out during December 1998 and January 1999 in the provinces of La Pampa, Córdoba, and San Luís.

STUDY AREA AND METHODS

Survey routes extended from Huanchilla, Córdoba in the north and Intendente Alvear, La Pampa in the east to the western border of La Pampa Province, approaching the Río Negro near the city of Neuquén in the province of Neuquén, Argentina (ca. 35°S, 64°W; Fig. 1). The climate becomes more arid from the eastern coast (Buenos Aires) to the mountains of western Argentina, with vegetation changing from agricultural grasslands to mesquite (*Prosopis* spp.) to desert-scrub grasslands. We chose four primary landscape divisions based on characteristics of the predominant vegetation type: agriculture, mixed agriculture/mesquite, mesquite, and desert-scrub grasslands.

The agriculture category consisted of a mix of cattle ranching and row-crop agriculture, with dominant summer crops of alfalfa, sunflower, sorghum, and corn. In the agricultural region, forests and shrubs exist intermittently, generally planted as shade areas for cattle, for wind breaks between fields, and as entrance corridors to estate houses. These forests most frequently consisted of groves of introduced eucalyptus (*Eucalyptus* spp.) trees. The mixed agriculture/mesquite category contained 25–75% mesquite, while the mesquite category contained

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