

A CHANGE IN FORAGING SUCCESS AND COOPERATIVE HUNTING BY A BREEDING PAIR OF PEREGRINE FALCONS AND THEIR FLEDGLINGS

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ABSTRACT.—The foraging habits of one pair of Peregrine Falcons (*Falco peregrinus*) nesting on a power plant in central Alberta were studied over seven consecutive breeding seasons (1998–2004). We observed 386 attacks that resulted in 117 captures of prey. The success rate increased from 21.9% in the first year to 39.1% in the seventh year and averaged 30.3%. The majority of hunts (76.7%) were initiated from soaring, and the peregrines commonly used the hot air above the plant's smoke stacks to gain height. The success rates of hunts launched from soaring versus perches were not significantly different (28.7% versus 35.6%). Tandem hunts by the pair ($N = 100$) were more successful than solo hunts (39.0% versus 27.3%), but the difference was not significant. The main prey species were Franklin's Gull (*Larus pipixcan*) and small passerines, which made up 53.0% and 27.4% of kills, respectively. There was a significant difference in the respective capture rates of these prey types (42.5% versus 24.1%). The success rates of the male and the female peregrines were not significantly different, but there was a notable difference in the prey taxa taken by each gender. The male captured 84.4% of the passerines, but only 22.9% of the gulls. After the first year, there was a significant switch from passerines to gulls, which paralleled a significant change in gender participation in foraging. All gulls captured by the male were surrendered to the female or to the fledged juveniles. In 23.3% of hunts, one or both parents were accompanied by one or more fledglings. The male participated in 76.7% of all parent-fledgling hunts ($N = 90$), the female in 10.0%, and the remainder by both parents. Aerial prey transfers from adults to flying young were feet-to-feet or through aerial drops. The hypothesis that parent peregrines make live-drops of prey to their fledged young to teach them how to hunt is confounded by observations that live-drops of just-caught prey are also made by the adult male to his mate. However, the hypothesis that peregrines assist their young in capturing prey is supported by anecdotal evidence.

KEY WORDS: *Peregrine Falcon*; *Falco peregrinus*; *tandem hunting*; *fledgling hunting*; *adult hunting*; *cooperative hunting*.

CAMBIOS EN EL ÉXITO DE FORRAJE Y CAZA COOPERATIVA EN UNA PAREJA DE *FALCO PEREGRINUS* Y SUS VOLANTONES

RESUMEN.—Se estudiaron los hábitos de forrajeo de una pareja de *Falco peregrinus* que anidó en una planta de energía en el centro de Alberta a lo largo de siete épocas reproductivas consecutivas (1998 a 2004). Observamos 386 ataques, los cuales resultaron en 117 capturas de presas. La tasa de éxito se incrementó del 21.9% en el primer año al 39.1% en el séptimo año, y en promedio fue del 30.3%. La mayoría de los eventos de caza (76.7%) fueron iniciados a partir de vuelos elevados; los halcones emplearon frecuentemente el aire caliente que se encontraba encima de las columnas de humo de la planta para alcanzar mayores alturas. La tasa de éxito de los ataques iniciados en vuelo no fue significativamente diferente de la de los ataques iniciados desde perchas (28.7% versus 35.6%). Los eventos de caza en los que ambos miembros de la pareja participaron en tándem ($N = 100$) fueron más exitosos que aquellos en los que participó un solo individuo (39.0% versus 27.3%), pero la diferencia no fue significativa. Las presas predominantes fueron la gaviota *Larus pipixcan* y varias aves paserinas pequeñas, representando el 53.0% y el 27.4% de las capturas, respectivamente. Existió una diferencia significativa en las tasas de captura de los distintos tipos de presa (42.5% para *L. pipixcan* y 24.1% para las aves

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paserinas). Las tasas de éxito no fueron diferentes entre el macho y la hembra, pero existió una notable diferencia en los taxa capturados por cada individuo. El macho capturó el 84.4% de las aves paserinas, pero sólo el 22.9% de las gaviotas. Después del primer año, existió un cambio significativo de paserinas a gaviotas de forma paralela con un cambio significativo en la participación de los miembros de la pareja en el forrajeo. Todas las gaviotas capturadas por el macho fueron entregadas a la hembra o a los volantones. En el 23.3% de los eventos de caza, uno o los dos padres estuvieron acompañados por uno o más volantones. El macho participó en el 76.7% de todas las cacerías en las que participaron volantones ($N = 90$), la hembra en el 10.0% de éstas, y ambos individuos en el porcentaje restante. Los adultos entregaron las presas a los juveniles en vuelo directamente de garras a garras, o dejándolas caer en el aire. La hipótesis de que los parentales dejan caer presas vivas para enseñarles cómo cazar a sus volantones es difícil de apoyar ya que el macho adulto también dejó caer presas recién capturadas en vuelo para que su pareja las tomara. Sin embargo, la hipótesis de que los peregrinos le ayudan a sus volantones a capturar presas es apoyada por información anecdótica.

[Traducción del equipo editorial]

Cooperative or tandem hunting by mated pairs of Peregrine Falcons (*Falco peregrinus*), in which both partners attack the same prey simultaneously, has been reported from many locations across the species' worldwide range (e.g., Cade 1960, Bird and Aubry 1982, Thiollay 1988, Frank 1994, Treleven 1998, Jenkins 2000). The success rate of tandem hunts has been reported to be higher than hunts by single peregrines (Thiollay 1988), but whether or not tandem hunting by mated pairs actually involves a degree of coordination between the two individuals is unclear. On their breeding range, Peregrine Falcons are also known to hunt together with their fledglings, although data are limited (Brown and Amadon 1968, Palmer 1988, White et al. 2002). The notion that juvenile peregrines need to be taught hunting skills by their parents is contradicted by the fact that captive-reared peregrines, deprived of parental instruction, begin pursuing and capturing prey at about the same age as young falcons at natural nest sites (Cade and Burnham 2003). Apparently, the peregrine does not need to be taught how to chase and kill prey (Cade 1982, Sherrod 1983). However, Newton (1979) and Ratcliffe (1993) state that more critical observation is needed during the period in which fledglings achieve independence.

This paper presents empirical data on the foraging behavior of one mated pair of peregrines hunting solo or in tandem over seven consecutive breeding seasons. Additionally, we present anecdotal observations on parent-fledgling interactions.

STUDY AREA AND METHODS

The study area is in central Alberta, Canada, at 53°N. In this largely agricultural region, peregrines nested commonly on cliffs and cutbanks along rivers and creeks until

they became extirpated (Dekker 1967, Fyfe 1976). A government program of releasing captive-reared peregrines in central Alberta began in 1975 and led to the establishment of breeding pairs on city buildings by 1981 (Holroyd and Banasch 1990). By the mid 1990s, peregrines began using nest boxes on high industrial structures in rural regions. The breeding site selected for this study is a power plant on the north shore of Wabamun Lake, which is roughly 8×20 km in size. The nest box was built by the Alberta Falconry Association in 1993 and put in place by TransAlta Utilities (Wabamun, Alberta) on a catwalk just below the top of a 91 m smoke stack. Lower down, the flat roof of the main building functions as a landing pad for newly-fledged young. Power line pylons in the vicinity provide high perches and plucking posts. Settling ponds and bare ground adjacent to the plant are used as loafing areas by the fledglings and by the adults that bring down large prey such as gulls and ducks. The landscape around the Wabamun plant is mainly wooded with small marshes and an extensive area (5–10 km²) of excavated and reclaimed terrain to the north. The lake receives light recreational use, and some shoreline sections are developed with cottages and small marinas.

The nest box is in plain view from a public road that runs between the lake and the plant. Depending on weather conditions, we watched from different vantage points 0.1–2 km away, and we used 8× wide-angle binoculars and 20–60× telescopes. Observation periods, lasting 3–6 hr each, usually between mid-afternoon and sundown, were spaced arbitrarily and increased during the period when the fledglings were on the wing. Over 7 yr, 1998–2004, the number of observation days was 196: 15 in June, 58 in July, 101 in August, 21 in September, and 1 in October. The only two days of observation in 1997 were added to the 1998 total. The median date when the first juvenile (always a male) fledged was 16 July (13–25 July). The number of young fledged was three or four per season with a mean of 3.6 ($N = 11$ males and 14 females). As indicated by their leg bands and plumage characteristics, the breeding pair consisted of the same individuals for the duration of the study, and we classified the female as a 2-yr old falcon in 1998 based on her brown dorsal color in 1997. The subspecific origin of these falcons is *F. p. anatum* and both originated from captive-reared stock nesting in the cities of Edmonton

and Calgary (Gordon Court, Alberta Environment, pers. comm.).

Prey species upon which peregrines are known to feed, such as waterbirds and small passerines, are common in the study area. With a mass of 220–335 g (Dunning 1984), the Franklin's Gull (*Larus pipixcan*) is close to the mass limit that male peregrines can or are willing to carry over long distances. Although Franklin's Gulls are locally scarce in early summer, large migrating flocks begin arriving in mid-July. Rock Pigeons (*Columba livia*), which are the dominant prey for peregrines in human altered environments (Ratcliffe 1993), were resident at the plant site but only in small numbers (<20).

The terms hunt and attack are used interchangeably and represent one attempt at capturing prey including one or more stoops or passes at the same target of which the outcome was known. Tandem hunts were simultaneous attacks by both adults on a flock of prey or an individual prey. Group hunts by a combination of parents and juveniles were tallied as adult hunts, and their kills were considered to have been made by the adults, although in a few cases it was the juvenile which actually seized (or was allowed to seize) the prey. Hunts by juveniles alone were not tallied.

Details of hunts and kills were entered into field diaries and annotated tabulations. Observer bias in comparing results between years, we believe, was not a factor as D. Dekker recorded observations over the 7-yr study period. R. Taylor was associate observer the last 3 yr of the project. Data sets were compared for significance by chi-square Test of Independence with a Williams' correction as described in Sokal and Rohlf (1981).

RESULTS

Hunting Methods and Prey Species. We observed 386 hunts by the adult peregrines. Nearly all (99.5%) were directed at airborne prey and consisted of two primary methods: attacks launched from soaring flight (76.7%) or from a perch (23.3%; Table 1). The falcons typically began a soaring sequence by circling up over the plant and using the hot air of the three stacks to gain height rapidly. Drifting downwind, the soaring falcons reached altitudes estimated to exceed 1000 m. By flapping their wings or gliding, they cruised upwind. Attacks on prey flying lower than the falcon were made by deep stoops with wings partly or fully flexed. Some of these attacks began with a burst of wing flaps and ended in a stoop, which could either be near-vertical or oblique. If the prey evaded the initial stoop, the falcon might follow up with one or more additional stoops or passes.

Still-hunting attacks were launched from high perches such as the catwalk railing near the top of the 91 m stacks. With rapid wing flaps, these falcons headed for targets some distance away (>100 m). After unsuccessful or aborted attacks, the peregrines commonly returned to the plant, either to

perch or to regain altitude by soaring. Some hunting sequences lasted 3–4 hr before a prey was captured. On other days, we observed falcons catch three prey in less than 1 hr.

The success rate of all hunts ($N = 386$) by the adult peregrines, either attacking prey solo or in tandem, was 30.3% (Table 1). Perch hunts were not significantly ($G = 0.77$, $P = 0.379$) more successful than soar hunts (35.5% and 28.7%, respectively). The success rate of the female was 37.1%, not significantly ($G = 2.37$, $P = 0.124$) different from that of the male (24.1%), but there was a notable difference in the taxa of the prey taken by the two sexes (Table 2). The male caught 84.4% of 32 small passerines, but only 22.9% of 62 gulls. Nearly all gulls seized by the male were released to his mate or a fledgling <1 sec after capture. If neither the female nor any of the fledglings were nearby, the male, upon seizing a gull, brought it down steeply and left it on open ground or on the roof of the plant ($N = 5$). The female carried gulls with apparent ease over distances exceeding 1 km.

The majority (84.9%) of gull kills observed at close range or found as prey remains ($N = 73$) were juveniles. Juvenile Franklin's Gulls were often seized in mid air during the falcon's first stoop. By contrast, adult gulls typically evaded a peregrine by rising steeply. Some evaded two or more additional passes and were eventually left alone. Others descended and plunged into water. In seven instances, the female peregrine repeatedly swooped at the swimming gull. Three were retrieved from the water and carried off. Some white birds, assumed to be gulls, that evaded 20 or more diving attacks far out over the lake may have been Common Terns (*Sterna hirundo*). Two terns were carried to the plant, but their capture had not been observed. Ring-billed Gulls (*Larus delawarensis*) were sometimes forced down, but we found no evidence that any were killed.

Rock Pigeons were seldom attacked. On two occasions, the female stooped unsuccessfully at free-flying flocks of pigeons. Both adults made opportunistic passes at pigeons that flushed from plant ledges below them, but the only successful pigeon hunts ($N = 2$) were initiated by fledglings. In at least one of these hunts, the capture was made by the adult female, who joined the attack.

During the sixth year of study, we gained the impression that the falcons had become more successful—in particular, at capturing gulls—than during the preceding years. This impression was

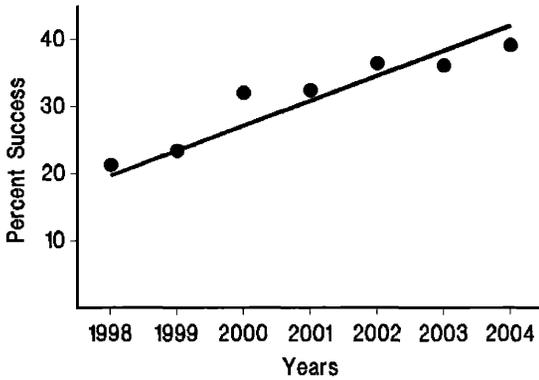


Figure 1. Hunting success per year of the same pair of Peregrine Falcons breeding in central Alberta, 1998–2004. The respective number of hunts/kills for the 7 yr of study were as follows: 108/23, 47/11, 25/8, 37/12, 44/16, 61/22, 64/25.

strengthened in year 7 and confirmed by subsequent data analysis. The overall success rate of the adults increased from 21.3% in the first year of study to 39.1% in the seventh year of study (Fig. 1).

Tandem Hunts. Each year from mid June onwards, both parents often began soaring together. The male gained height quicker and always circled higher than the female. Stooping alternately, they attacked 68 prey from soaring flights (Table 1). If no prey had been sighted for some time, the pair separated or headed off into the distance, one following the other, either in soaring or flapping flight. Tandem attacks were also launched from high perches on the plant. In tandem attacks, both falcons could take the lead, and the male flew higher than the female. While the female approached the prey directly, the male typically attacked from above in a near vertical stoop. A high percentage (60–75%) of tandem hunts were lost from view before we could either see the target or the result. Tandem hunts of which the outcome

was known ($N = 100$) represented 25.9% of all hunts, and their success rate was higher than in 286 solo hunts (39.0% versus 27.3%), but the difference was not significant ($G = 2.39$, $P = 0.121$). The success rate of 32 tandem attacks launched from a perch was 50.0%, compared to 33.8% for tandem attacks from soaring position.

Tandem hunts resulted in 39 kills (Table 1). Of these, 26 captures of prey were observed in detail: seven were seized by the female, 19 by the male. Prey caught by the male in tandem attacks were surrendered at once to the female, either by feet-to-feet transfer ($N = 5$) or released in the air ($N = 14$). Thirteen of these aerial drops were gulls, which resumed flight upon release. Nine were subsequently seized by the female; four evaded her passes and were let go or escaped by splashing down into water.

Hunts by Groups of Adults and Fledglings. In 23.3% of hunts ($N = 386$), one or both parents were accompanied, and often harassed, by one or more juveniles (Table 3). Some fledglings closely followed the adults prior to the start of a hunt, others approached hurriedly from a distance to join a hunt in progress. A significant majority of group hunts ($G = 37.96$, $P = 0.001$) were led by the adult male, which made 71.0% of the 31 kills (Table 3). Prey caught by the parents were transferred, usually at once, to the approaching juveniles, either by feet-to-feet transfers ($N = 15$) or through aerial drops ($N = 7$). At least three small passerines that were dropped were still alive and resumed flight. They were recaptured by a juvenile or by the adult and released again. Three live-drops were gulls. In addition, four of 11 gulls caught in adult-juvenile hunts were seized in flight by the juveniles “chaperoned” by adults.

After successful group hunts, one or more juveniles fed on the kill. If the feeding site was in an open area away from the plant, the adult female typically perched on a pole nearby ($N = 14$). At

Table 1. Hunts and kills made by a pair of Peregrine Falcons nesting on a power plant in central Alberta, 1998–2004. The hunting success rates are presented in parentheses.

	HUNTS/KILLS FROM SOARING	HUNTS/KILLS FROM PERCH	TOTAL HUNTS
Adult male (24.1%)	176/44 (25.0%)	40/8 (20.0%)	216/52
Adult female (37.1%)	52/18 (34.6%)	18/8 (44.4%)	70/26
In tandem hunts (39.0%)	68/23 (33.8%)	32/16 (50.0%)	100/39
Totals (30.3%)	296/85 (28.7%)	90/32 (35.5%)	386/117

the approach of people, she vocalized and "swooped" overhead. She also stooped at crows or *Buteo* hawks, apparently to drive them away. After the fledglings were satiated and left, the adult female sometimes fed on the remains of the kill ($N = 5$).

DISCUSSION

Hunting Success. The hunting success of adult peregrines on breeding territory is generally higher than that of migrating or wintering peregrines (Dekker 1980, Roalkvam 1985). Jenkins (2000) compared data presented in eight publications on breeding peregrines and found an extreme variation (9.3–84.1%) in hunting success, but much less variation in hunting methods. The majority (58–75%) of attacks summarized in his review were launched from a perch. By contrast, the percentage of perch hunts was only 23% at Wabamun. The "still-hunting strategy" of perch hunts reduces the energy cost of foraging. However, high-soaring flight is also relatively energy-efficient and widens the radius of the attack zone (Enderson and Craig 1997). Soaring flight has been reported as a common hunting method in many regions, but not to such a high degree as documented in this study. The second highest use was recorded in Africa, where breeding pairs launched 30–42% of hunts from flight (Thiollay 1988, Jenkins 2000). The use of factory exhaust to facilitate soaring flight by the Wabamun peregrines was described in an earlier publication (Dekker 1999), but this phenomenon has to our knowledge not been reported elsewhere.

It is noteworthy that the falcons in this study attacked nearly all of their prey in flight, often at great altitudes. This is in sharp contrast to migrating or wintering peregrines, which commonly use surprise methods to attack prey on the ground or in shallow water (Dekker 1980, 2003, Cresswell 1996). However, there is also an element of surprise involved if a soaring peregrine stoops from a great height at prey flying far below. In solo hunts, the male frequently made long stoops that levelled out low over woods and were aimed at flocks of small passerines flying just beyond the trees. Surprise is probably also a factor in tandem hunts in which the male stoops from high above while the female pursues the prey at a lower altitude.

A key factor in the hunting success of peregrines is the vulnerability of individual prey, which is difficult to assess for the human observer. It is well-

known that predation risk for land birds increases over water (Herbert and Herbert 1965). Conversely, water birds become vulnerable over land (Hunt et al. 1975, Dekker 1980). Mature prey on home territory should be harder to catch for a raptor than juvenile prey passing over unfamiliar terrain. In central Alberta, the migrations of juvenile prey species approximately coincide with the period when fledgling peregrines are on the wing and when the parental task of provisioning them is most demanding. In this study, the peregrines were very successful at capturing juvenile Franklin's Gulls. For instance, on 7 d between 17 July and 9 August 2003, when thousands of gulls were passing through the area, the adult female, hunting solo, captured each of seven juvenile gulls in her first attack of the afternoon and each requiring only one stoop. While it does not seem surprising that bird-hunting falcons should become better at what they do as they become older and gain in experience, data in support of that notion have, to our knowledge, not been published before. An explanation for the year-to-year increase in the success rate of the Wabamun pair is that these falcons became specialists on juvenile Franklin's Gulls, which differ from adults by their dusky color and absence of black on the head. Juvenile targets were probably pre-selected before the falcons began their attack. A similar pre-selection hypothesis was advanced for the high success rate (73–93%) of "Red Baron," an adult male peregrine hunting over coastal marshes in New Jersey (Cade and Burnham 2003:333).

In this study, the prey component changed significantly after the first year (Tables 4 and 5). In the first year of study, gulls made up only 8.7% of kills compared to 63.8% in years 2–7 ($G = 10.85$, $P = 0.001$). The proportion of small passerines changed significantly from 60.9% in the first year to 19.1% in years 2–7 ($G = 7.01$, $P = 0.008$). Overall, the capture success on gulls (of both age groups) was significantly higher ($G = 5.35$, $P = 0.021$) than on small passerines (42.5% versus 24.1%). Successful taking of juvenile gulls may be even higher than for adults, but an adequate sample was not available for adults. As reported in results, the sample of gull kills ($N = 73$) included 84.9% juveniles.

Coincident with the observed prey switch, we recorded a major change in foraging participation between the sexes after the first year (Table 6). The male's solo hunts in the first year were 78.7%

Table 2. Prey taxa captured by the Peregrine Falcon pair hunting solo or in tandem.

	FRANKLIN'S GULLS	SMALL PASSERINES	SMALL SHOREBIRDS	DUCKS	OTHER OR UNIDENTIFIED
Adult male	14	27	1	1	9
Adult female	21	2	1	2	0
Pair in tandem	27	3	5	0	4
Totals	62	32	7	3	13

of total hunts ($N = 108$), significantly greater ($G = 8.08$, $P = 0.004$) than the 47.1% of hunts in years 2–7 ($N = 278$). By contrast, the female's share during the first year was 2.7%, and this rose significantly to 24.1% in years 2–7 ($G = 23.51$, $P = 0.001$). A possible explanation is that the female lacked skill and experience in her first year on territory. As she became older and gained expertise, she began to play a more active role in foraging. There was no significant change ($G = 2.70$, $P = 0.1$) in the proportion of tandem hunts between the first year and years 2–7 (Table 6).

Our findings that the primary prey of the male was passerines, whereas the female's main prey was gulls (Table 2), lends support to the hypothesis that the reversed sexual size dimorphism in raptors such as seen in the peregrine allows them to exploit a wider prey base and reduces competition between the sexes (Selander 1966).

Cooperative Hunting. Are peregrines that attack the same prey simultaneously with their mates or fledglings actually cooperating? Or, are the individuals simply reacting at the same time to the stimulus of sighting prey? True cooperative hunting differs fundamentally from other forms of group predation, such as pseudo-cooperative hunting (Ellis et al. 1993). In true cooperative hunting, the group consists of at least two members that are a stable social unit, and their cooperation should benefit the group rather than just the individual. An example of true cooperative foraging is described by Bednarz (1988) for the Harris's Hawk

(*Parabuteo unicinctus*). Ellis et al. (1993) conclude that cooperative hunting is the most efficient strategy for capturing prey in many situations and that each form of social foraging should have evolved as an adaptive advantage enhancing the fitness of all individuals in the group. In the Aplomado Falcon (*Falco femoralis*), pair hunting is more than twice as productive as solo hunting when the prey are birds (Hector 1986). Similarly, the success rate of pair hunting in peregrines may depend on the species of prey hunted (Jenkins 2000).

In this study, tandem hunts by the mated pair of peregrines were more successful than solo hunts (39.0 versus 27.3%), although the difference was not statistically significant. Moreover, the individual success rate of the two partners in tandem hunts is actually halved. So what, if any, is the fitness value of tandem hunting for this pair of breeding peregrines? It may lie in the fact that any action by the male that benefits his mate or their progeny should be of adaptive advantage.

At Wabamun, the adult male was not seen to eat the gulls he killed, although on two occasions he fed on gull remains abandoned by fledglings. The fact that he mainly hunted such prey in the company of his mate or fledglings suggests that his role was a cooperative one. This view is supported by anecdotes such as the following. By mid September 1999, after the fledglings had dispersed, the adults were still hunting together. One evening, shortly after both had soared up over the plant, the male caught a small passerine and landed on a pylon to

Table 3. Hunts/kills made by one or both Peregrine Falcon parents accompanied by one or more fledgling juveniles.

	1 JUVENILE	2 JUVENILES	3 JUVENILES	TOTALS
Adult Male	29/10	34/10	6/2	69/22
Adult female	3/2	6/4	0/0	9/6
Both adults	6/3	5/0	1/0	12/3
Totals	38/15	45/14	7/2	90/31

Table 4. Prey captured by a pair of Peregrine Falcons as a percentage of total prey per year.

YEAR	PERCENT GULLS	PERCENT PASSERINES	PERCENT OTHER	NO. TOTAL PREY	NO. HUNTS
1	8.7	60.9	30.4	23	108
2	63.6	27.3	9.1	11	47
3	62.5	12.5	25.0	8	25
4	58.3	16.7	25.0	12	37
5	43.7	31.3	25.0	16	44
6	63.6	27.3	9.1	22	61
7	80.0	4.0	16.0	25	64
Totals	53.0	27.4	19.6	117	386

consume his prey. Instead of interfering, the female perched on the next pylon and waited for her mate to finish his meal. Presently, both soared up again and eventually flew out high over the lake, stooping in tandem at gulls. Like many similar observations, this incident suggests that the male's role was truly a cooperative one—to assist his mate in her foraging.

The question of whether attacks on the same prey by a combination of adults and fledglings can be considered cooperative seems even less clear, for it is apparent that the juvenile is primarily intent on kleptoparasitizing the adult. If there is cooperation, it is one-sided and benefits only the juveniles (i.e., this may be considered as parental investment). Nevertheless, the evolutionary value of adult/fledgling combinations is undeniable, as a well-fed progeny enhances the future of the family genes. In support of the hypothesis that the participation of adults in joined hunts with their fledglings indeed represents parental care, we present a number of anecdotal observations in the appendix.

Live-drops of Prey. Cade (1982) and Sherrod (1983) characterize the behavior of paired male peregrines in social interactions with their bigger mate as submissive and even fearful. Females take food from males in an aggressive manner, not only

during the breeding season but also on migration or at the wintering grounds. Unmated females routinely force males to drop just-caught prey (Dekker 1980, 2003). Tandem hunting by unmated peregrines is relatively common and driven by competition rather than cooperation. Two or more (up to six) migrating or wintering peregrines were seen in joint pursuit of the same prey in Alberta and British Columbia. Male peregrines were forced to make live-drops of prey not only to female conspecifics, but also to other kleptoparasitic raptors, such as Prairie Falcons (*Falco mexicanus*) and Bald Eagles (*Haliaeetus leucocephalus*; Dekker 1995, 1998).

I concur with Sherrod (1983) that the release of just-caught prey by the male peregrine at the approach of an aggressive female may be triggered by the impulse to avoid close contact. The importance of a timely release was demonstrated on 21 August 2003, when the Wabamun male, carrying a just-caught prey and flying 20–25 m high, was met by a screaming juvenile female in typical begging flight. Apparently, the male was just too late in releasing his prey, for he was seized by the juvenile. Locked by their feet, both birds tumbled about 15

Table 5. Comparison of main prey taxa captured by a pair of Peregrine Falcons in study years 1 and 2–7.

	PREY TAXA	NO. KILLS	PERCENT OF TOTALS	
			KILLS	N
Year 1	Gulls	2	8.7	23
Years 2–7		60	63.8	94
Year 1	Passerines	14	60.9	23
Years 2–7		18	19.1	94

Table 6. Number of hunts by the adult male and female, either hunting solo or in tandem, in year 1 and years 2–7.

		NO. HUNTS	PERCENT OF TOTAL
Year 1	Adult male	85	78.7
N = 108 hunts	Adult female	3	2.7
	Tandem	20	18.5
Years 2–7	Adult male	131	47.1
N = 278 hunts	Adult female	67	24.1
	Tandem	80	28.8

m before separating again, while the prey item fell into the bushes below and was lost.

Based on a thorough review of the literature and on his own studies, Sherrod (1983) observed that the behaviors of parents and fledglings complement each other. While the youngster only wants food, the adult appears to be very willing to supply that food. Some live-drops are no doubt the result of the aggressive approach of the begging falcon. However, as argued by Newton (1979), other live-drops are clearly intentional as parent peregrines will recapture the live-dropped prey and release it again if the fledgling fails to catch it the first time. Such repeat drops were seen in this and other studies (Frank 1994, Treleaven 1998).

CONCLUSION

Some of the aerial drops of just-caught and still live prey from adult to fledgling (described in the appendix) lend support to the hypothesis that the parents were teaching their young by example. Although young falcons do not need to be taught to hunt, such extended parental care might well give them a certain survival advantage after leaving the nest site. The observation that live-drops were also made from adult to adult, both at Wabamun and at a natural nest site in northern Alberta (Dekker 1999), may seem to refute the above hypothesis. Because there can be no doubt that adult females are accomplished hunters, the male's reason for making live-drops to his mate can have nothing to do with teaching. However, here a secondary and complementary factor comes into play. Whether hunting with his mate or a fledgling, the male plays a dual role, either in support of his mate or progeny.

It is difficult, if not impossible, to translate all of the anecdotes detailed in the appendix into hard data in support of the teaching hypothesis. As to the alternative, but not exclusive, hypothesis that parent peregrines assist their fledglings in capturing their first prey, on the evidence presented here, we are convinced that the answer is affirmative.

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- below. Seconds later, a juvenile female stooped from above, just missing the gull. The adult male then stooped again, just short of the target. Chased by both peregrines, the gull eventually escaped. In this case, as in others, it seemed clear that the male did not want to catch the gull himself. Instead, he attempted to set it up for the approaching juvenile.
- (2) On two occasions, when a gull was chased by a group of one adult and one fledgling, the adult hit or touched the prey, causing it to cartwheel in the air. In the next instant, the gull was seized by the closely-following juvenile. Our impression was that the adults were not intent on taking the gull themselves.
- (3) On 12 August 2000, the adult male, while soaring in tandem with his mate, suddenly sprinted away (400–500 m) to hit a shorebird that was being chased by two juveniles at an altitude estimated at 75 m. Dead or stunned, the prey fell into reeds and was lost before the juveniles could recover it. This was one of only four instances when these peregrines hit their prey in the air, as opposed to the common method of binding to the prey and carrying it down. The remarkable point is that the adult male did not stoop and recover the plunging shorebird himself, which would have been a normal procedure if he had been hunting alone.
- (4) A Rock Pigeon pursued by a fledgling was taken by the adult female, who transferred it at once to the juvenile. On their own, the adults seldom pursued pigeons.
- (5) Fledglings that have been on the wing for only a few days have difficulty carrying a gull. After making an aerial transfer to an unskilled juvenile, the adults will accompany it in flight and retrieve the gull if dropped. By the same token, seemingly aware of the lack of ability in a badgering female youngster, the adult female refused to transfer a just-caught gull and instead carried it ca. 500 m to the roof of the plant, where she at once surrendered it to the fledgling.
- (6) The adult male demonstrated an awareness of the different needs of the genders. In group hunts with male offspring, he selected mostly passerines or small shorebirds (41 of 45). By contrast, he usually attacked gulls in the company of females. After capturing one or more gulls for his mate or the fledglings, he hunted smaller prey for himself.
- The above interactions between parents and fledglings parallel numerous anecdotes described by long-term peregrine observers in New York and Great Britain (Frank 1994, Treleven 1998).
- It is our impression that adult peregrines appear to know how to assist their progeny in gaining independence. For a start, there is a change in food exchanges when the first of the juveniles are close to fledging. Both at Wabamun and a natural nest site in central Alberta, the adult male appeared to coax a fully-feathered male youngster to fly. Instead of transferring the prey item in the usual direct manner, he cruised back and forth just

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APPENDIX. Observations of parental care by a pair of peregrines toward their fledglings and nearly-fledged juveniles.

(1) On 16 August 1999, having stooped at a gull and missed his target, the adult male maneuvered under it in a peculiarly slow flying style. He appeared to drive the gull upward and prevent it from dropping into the water

out of reach, holding the prey in his lowered feet. His behavior cannot be explained as having been prompted by fear of a bigger bird for this incident involved a male juvenile. After the young male failed to fledge, the adult gave the food item to another juvenile, a fully-feathered female sitting on the catwalk. Similarly, on two other occasions when he arrived with a small prey, he flew right up to a screaming juvenile male that was perched on the edge of a catwalk, but instead of exchanging the prey feet-to-feet, he dropped it and recovered the falling item in a quick stoop. He repeated this teasing show three or four times. After the fully-feathered juvenile male failed

to fly, the adult gave the food item directly to a less-developed female still in the nest box.

Another noteworthy exchange involved the female. One day, after she had delivered a prey to two juvenile males, which shared the food, the male arrived, also with prey. He gave it directly to one of the same two youngsters. Instantly, the adult female interfered. She took the food item away from the young male and offered it instead to a juvenile female which had not been fed for several hours. Similar incidents were seen at Wabamun and at a natural nest site in central Alberta (D. Dekker unpubl. data).