EFFECTS OF EXPERIMENTAL NESTLING HARVEST ON PRAIRIE FALCONS

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Abstract: Prairie falcons (Falco mexicanus) are harvested (removed from wild populations) for falconry, and state resource agencies set harvest limits and issue harvest guidelines, yet managers lack information on effects of harvest on prairie falcon populations. We examined effects of long-term nestling harvest on prairie falcons by comparing subsequent territory occupancy, nesting success, productivity, and breeder and nestling return frequencies between experimentally harvested and nonharvested territories in southwestern Wyoming, 1982-89. The percentage of territories occupied by breeding adults the following year was higher ($P = 0.10$) for harvested territories compared with nonharvested territories. Subsequent nesting success was lower ($P = 0.03$ and 0.09) on harvested territories compared with nonharvested territories in 2 of 7 years after harvesting began, but did not differ ($P = 0.31$) with all 7 years pooled. Productivity was lower ($P = 0.03$) within harvested territories compared with nonharvested territories in 1983, but did not differ ($P = 0.84$) when all years were pooled. Return rate of territorial breeders was lower on harvested compared with nonharvested territories ($P = 0.04$). Fledglings from harvested territories returned as breeders more frequently ($P = 0.09$) than fledglings from nonharvested territories. Results suggested that intensive harvest of nestling prairie falcons may adversely affect some local population parameters, but harvests were sustainable and probably did not affect local population size.

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Accurate estimates of population parameters, such as reproductive success, recruitment, territory fidelity, and dispersal, are critical for managing harvested populations to ensure that harvest is commensurate with the population's ability to sustain itself. Fluctuations in population parameters are the most appropriate measures of the effects of environmental changes or human disturbance on bird populations compared with more typical measures of abundance and distribution (Temple and Wiens 1989, Martin 1992). Time lags in response of birds to environmental changes must be expected and are pronounced in species with high territory fidelity (Temple and Wiens 1989), yet long-term studies examining effects of disturbance on animal population parameters are rare. Monitoring effects of harvest is particularly important in territorial species with high site fidelity because disturbance may cause territory abandonment.

Harvesting raptors for falconry was legal in 42 states, and 2,500-3,000 people practiced falconry nationally (Brohn 1986, U.S. Dep. Inter. 1987). Approximately 1,000 raptors (600—1,600) were harvested annually from the wild for falconry, and 12–21% of the recorded raptor harvest was prairie falcons, making them the second most commonly harvested species (Brohn 1986). Prairie falcons were harvested in 19 states and most harvested birds were taken as nestlings or young birds (Brohn 1986, U.S. Dep. Inter. 1987). State resource agencies set annual prairie falcon harvest limits and issue harvest guidelines, yet they often lack information on effects of harvest on falcon populations. Prairie falcons are specialized, territorial raptors (Runde and Anderson 1986, Steenhof and Kochert 1988) exhibiting high nesting site fidelity (Platt 1981, Steenhof et al. 1984, Runde 1987) that renders

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them vulnerable to chronic disturbance. We examined the effect of harvesting nestlings on a prairie falcon population by comparing subsequent territory occupancy, nesting success, productivity, and rates of breeder and local fledgling return between experimentally harvested and nonharvested territories.

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STUDY AREA AND METHODS

The study area was in north-central Sweetwater County, Wyoming, at 1,980–2,600 m elevation, with annual precipitation of 18–23 cm. The area was approximately 3,420 km^2 of sagebrush (Artemisia spp.) steppe rangeland (Kuchler 1964) with a variety of cliffs, canyons, and buttes upon which falcons nested. For descriptions of soils and vegetation, see Severson (1966) and Runde (1987).

We delineated a 1,100-km^2 portion of the area as the harvest area. This area was representative of the overall study area in vegetation, topography, and level of disturbance, but contained 20 prairie falcon nesting territories in 1982 compared with 40 nesting territories in the adjacent nonharvest area. We defined nesting territory as an aerie and its surroundings where only 1 pair had bred at 1 time (Newton and Marquiss 1982, Allen 1987, Steenhof 1987). We simulated a legal falconry harvest by removing nestlings from nesting territories having >1 chick, with the goal of suppressing post-harvest productivity to ≤ 2 young fledged/occupied territory. We harvested nestlings at 21–35 days and fostered them to active prairie falcon nests in eastern Wyoming or gave them to licensed falconers. We defined productivity as the mean number of young per occupied territory at 21 days post-hatch (Steenhof 1987). Mean clutch size varied annually ($\bar{x} = 4.23$, SD = 0.43, range 3.64–4.85) (Conway et al. 1993). We chose 2 young/occupied territory because we wanted post-harvest productivity to be consistent among years. Consequently, the actual number of nestlings harvested varied annually and depended on the number of nestlings per occupied territory prior to harvest.

We surveyed all cliffs throughout the study area by helicopter starting in late March each year, 1982–89. We also surveyed from the ground all potential nesting cliffs from March through May of each year. We located occupied prairie falcon territories by observing territorial behavior or activity near a cliff. We revisited territories during ground surveys from late May through July to confirm occupancy and determine productivity. We trapped adult falcons using mist nets and Dho-gaza nets with a live great horned owl (Bubo virginianus) decoy on nesting territories. We climbed to all prairie falcon nests after chicks hatched to determine reproductive stage and returned to band adults and nestlings with U.S. Fish and Wildlife Service aluminum bands and determine sex of nestlings (Moritsch 1983) when nestlings were 3–5 weeks old. We reduced productivity within 20 territories by removing 3–5-week-old nestlings in 1982–89 so that mean number of young fledged per occupied territory was 1.86 (SD = 0.09). In 1983, we did not remove any nestlings because natural productivity in the harvest area was 1.61 nestlings/occupied territory. Research disturbance was equal between harvested and nonharvested territories. We visited nonharvested nests once to confirm occupancy and once to band nestlings. When harvesting young, we attempted to maintain natural nestling sex ratios.

We compared occupancy, nesting success, and productivity between harvested and nonharvested territories. We calculated occupancy rate as the proportion of traditional territories occupied by pairs in a given year, and we defined traditional territories as those occupied in 1982 (Steenhof 1987). We located additional occupied territories in subsequent years (Conway et al. 1993), but these were not included in analyses because of bias associated with first-year occupancy. Using the Mayfield method (Mayfield 1975, Hensler and Nichols 1981), we calculated the daily probability of nest survival and percent nesting success of harvested and nonharvested territories. We considered a breeding pair successful if it produced ≥ 1 young that reached 21 days of age (Steenhof 1987). Productivity of harvested territories included harvested nestlings (preharvest productivity).

We calculated return rates for each sex, for

Table 1. Occupancy rate within experimentally harvested and nonharvested prairie falcon breeding territories, southwestern Wyoming, 1982-89.

Year	Harvested (n = 20)	Nonharvested (n = 40)	χ^2	*P*
1983	0.90	0.89	0.01	0.95
1984	1.00	0.84	3.52	0.06
1985	0.80	0.80	0.00	1.00
1986	0.75	0.61	1.22	0.28
1987	0.80	0.58	2.97	0.09
1988	0.80	0.82	0.03	0.88
1989	0.75	0.76	0.01	0.95
1983–89	0.83	0.75	2.69	0.10

harvested and nonharvested territories, as the percentage of marked breeders present in year t that also were present in year t + 1. We calculated fledgling return rates as the number of locals of each sex hatched and banded on the site that were recaught as breeders divided by the total number of new breeders captured on territories. These proportions represent minimum estimates for natal recruitment because some nestlings were not banded. We also calculated the proportion of banded fledglings from harvested and nonharvested territories that returned to our study area as breeders.

We tested variables for normality by examining Shapiro-Wilk's W-statistics and normal probability plots (SAS Inst. Inc. 1985). We compared occupancy rate, return rate, and proportion of fledglings returning as breeders between harvested and nonharvested territories with Chi-square goodness-of-fit tests (Zar 1984). We compared estimates of nesting success between harvested and nonharvested territories using the Chi-square statistic (program CONTRAST; Sauer and Williams 1989). We compared productivity between harvested and nonharvested territories with t-tests (Zar 1984). Because we wanted to limit our sample size of experimentally harvested nests, yet ensure that we could detect a harvest effect if one existed, we used a = 0.10 for all comparisons.

RESULTS

We removed 138 of 451 nestlings ($\bar{x}$ = 17.3 nestlings/year, SD = 13.2) from 20 territories during 1982–89. The number of years each territory was harvested varied according to territory occupancy and productivity: 1 year (n = 3 territories), 2 years (n = 4), 3 years (n = 8), 4 years (n = 4), and 5 years (n = 1). Harvest never caused territory abandonment in the year of harvest.

All variables were normally distributed (W > 0.93, P > 0.30, Shapiro-Wilk's test). Subsequent occupancy of harvested territories was slightly higher than that of nonharvested territories (Table 1). We did not detect a difference in subsequent nesting success between harvested and nonharvested territories with all 7 years pooled (Table 2). However, there was evidence (χ^2 = 12.98, 7 df, P = 0.073) of among year heterogeneity in nesting success within harvested territories. Consequently, we compared nesting success between harvested and nonharvested territories for each year separately. Nesting success in harvested territories was lower than in nonharvested territories in 1983 and 1985 (Table 2).

We did not detect a difference in mean productivity between harvested and nonharvested territories with all years pooled (Table 3). However, there was among year heterogeneity (F = 3.80; 7, 132 df; P < 0.001) in mean productivity

Table 2. Maylield estimates of percent nesting success using maximum likelihood estimators (MLE), daily nest survival (p), and standard error (SE) of daily nest survival within experimentally harvested and nonharvested prairie falcon breeding territories. southwestern Wyoming. 1982-89.

Year	Harvested				Nonharvested				χ^2	P[b]
	MLE	$\hat{p}$	SE	n[a]	MLE	p	SE	n[a]		
1983	40	0.9885	0.004	17; 784	79	0.9971	0.001	25; 1,371	4.5	0.03
1984	74	0.9962	0.002	17; 1,039	82	0.9974	0.002	19; 781	0.2	0.62
1985	49	0.9910	0.003	18; 774	81	0.9973	0.002	26; 1,125	2.9	0.09
1986	65	0.9945	0.003	15; 549	52	0.9918	0.004	15; 485	0.3	0.59
1987	100	1.00	0.037	17; 722	100	1.00	0.037	18; 746	0.0	1.00
1988	100	1.00	0.030	17; 1,088	85	0.9979	0.001	26; 1,432	0.0	1.00
1989	92	0.9990	0.001	17; 983	70	0.9956	0.002	23; 1,127	2.4	0.12
1983–89	73	0.9959	0.001	118; 5,939	79	0.9970	0.001	152; 7,067	1.0	0.31

[a] No. of nests; no. of obs. days.
[b] Chi-square tests for differences in nesting succes between harvested and nonharvested territories (program CONTRAST, Sauer and Williams 1989).

Table 3. Number of young fledged per occupied territory within experimentally harvested and nonharvested prairie falcon breeding territories, southwestern Wyoming, 1982–89.

Year	Harvested[a]			Nonharvested					
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	t	P[b]	Power[c]
1982	2.15	1.87	20	2.68	1.91	28	0.95	0.35	0.24
1983	1.61	2.03	18	2.83	1.78	30	2.18	0.03	
1984	2.11	2.11	19	2.00	1.81	31	0.19	0.85	0.17
1985	2.63	2.00	16	2.96	1.83	27	0.57	0.57	0.25
1986	2.71	2.16	14	2.79	2.12	19	0.10	0.92	0.18
1987	4.13	0.83	15	3.44	1.46	16	1.62	0.12	0.47
1988	3.44	1.46	16	3.35	1.70	26	0.18	0.86	0.37
1989	3.60	1.30	15	2.60	2.12	25	1.65	0.11	0.22
1982–89	2.73	1.92	133	2.78	1.87	202	0.25	0.80	0.84

[a] Includes harvested nestlings.
[b] 1-tests for differences in no, of young fledged/occupied territory between harvested and nonharvested territories.
[c] Power $(1 - \beta)$ of detecting a difference of $\gamma > 0.80$ (γ = the proportional difference in productivity between nonharvested and harvested territoricr we wished to detect)

within harvested territories (Table 3). Consequently, we compared mean productivity between harvested and nonharvested territories for each year separately. Mean productivity in harvested territories was lower than in nonharvested territories in 1983, but we did not detect differences in the other 7 years (Table 3). We approximated the power of these tests at an a = 0.10 for y = 0.8, the proportional difference in mean productivity we wished to detect. We assumed that mean productivity in harvested territories equaled y times the mean productivity in nonharvested territories, based on the premise that productivity might be lower in harvested territories. Power for detecting differences was <0.5 in annual comparisons but >0.8 for the 8-year pooled comparison (Table 3).

We captured 71 adult males and 125 adult females on territories from 1982 to 1989. We recaptured 71 adult falcons in ≥2 years. Return rate was lower (χ^2 = 4.14, 1 df, P = 0.04) on harvested territories (14 of 26) compared with nonharvested territories (26 of 33), but did not differ (χ^2 = 0.774, 1 df, P > 0.50) between males (10 of 17) and females (29 of 41). On 147 territories from 1982 to 1989 where ≥1 breeding adult was trapped, 19 had a new, unmarked individual, 39 had the same individual, 69 had an unidentified breeding adult, and 20 were vacant the following year.

At least 1,042 young reached fledging age and 652 banded young fledged during our 8-year study (Conway et al. 1993). Of 451 fledglings banded before 1988, we subsequently recaptured 10 occupying breeding territories. Of these 10, 1 was a 1-year-old male, 5 were 2-year-old birds (4 M, 1 F), and 4 were 3 year olds (1 M, 3 F). The 1-year-old male occupied a territory but nested unsuccessfully. Fledglings from harvested territories (7 of 196) returned as breeders more frequently (χ^2 = 2.93, 1 df, P = 0.09) than fledglings from nonharvested territories (3 of 255).

DISCUSSION

Experimentally harvested territories had higher occupancy rates, but similar productivity compared with nonharvested territories. Occupancy rates of harvested and nonharvested territories were similar to those reported (47–98%) elsewhere (Enderson 1964, Fyfe et al. 1969, Edwards 1973, Parker 1973, Ogden and Hornocker 1977, Runde 1987, Lanning and Hitchcock 1991). Partial harvest may have caused increased local occupancy rates by increasing fledgling survival (because of decreased sibling rivalry and increased parental investment/fledgling), resulting in increased local recruitment of philopatric young. Productivity was higher than that reported ($\bar{x}$ = 1.15 young/occupied territory) for Colorado and Wyoming (Enderson 1964), but within the range (1.9–3.4 young/occupied territory) reported from other regions (Enderson 1964, Olendorff and Stoddart 1974, Ogden and Hornocker 1977, Runde 1987).

Although harvest may initially increase territory occupancy, harvested territories may be occupied by new, inexperienced breeders. Indeed, subsequent nesting success was lower on harvested territories compared with nonharvested territories in 2 of 7 years. The estimated proportion of breeding prairie falcons returning to the same territory the following year was 67%

(39 of 58), which is greater than breeder return rates (2 and 43%) reported elsewhere (Enderson 1964, Ogden and Hornocker 1977). However, breeders on harvested territories had a lower return rate compared with breeders on nonharvested territories; therefore, harvest may decrease territory fidelity. Nesting raptors may still fledge young when disturbed, but may not reuse the territory the following year (Fyfe and Olendorff 1976, Platt 1977, White and Thurow 1985).

We did not detect sex differences in fledgling return rates, but young fledged from harvested territories returned to breed on our studv area more frequently than young fledged from nonharvested territories. Prairie falcons and other raptors usually breed in the vicinity of their natal areas (Newton 1979, Newton and Marquiss 1983, Steenhof et al. 1984), and survival of first-year birds is often low. The higher fledgling return rate from harvested territories in our study may reflect increased first-year survival resulting from decreased sibling competition or a facultative increase in philopatry in response to decreased local productivity. If nestling harvest causes increased fledgling survival, harvesting practices may benefit local populations by increasing local recruitment. However, if harvest causes increased fledgling return rates, natal dispersal decreases and genetic mixing and population expansion capabilities necessarily decrease.

MANAGEMENT IMPLICATIONS

We used a liberal a-level (0.10) for comparisons; consequently, our results should be interpreted cautiously and further studies should attempt to replicate our results. There is also a need to explain why occupancy rate is higher in harvested territories and to better examine effects of harvest on breeder dispersal and philopatry. Populations may respond to harvest in different ways depending on density, the degree of territory fidelity, and availability of suitable nesting sites, all of which were high in our study area.

Falconers harvested approximately 0.2% of the prairie falcon population annually (Brohn 1986, U.S. Dep. Inter. 1987). Prairie falcons are popular with falconers because of their accessibility (U.S. Dep. Inter. 1987), and in some areas harvest pressure is probably concentrated on nestlings in several accessible traditional aeries known to falconers. Occasional harvest of 1 prairie falcon nestling from a traditional territory probably does not adversely affect future use or productivity. Continual harvest of >1 falcon nestling from multiple territories in a population can affect population parameters, but harvest demands in 1988 of prairie falcons for falconry (0.2% of population, nationally) was sustainable and inconsequential to the population (U S Dep. Inter. 1987). Continued harvest of the same territories may cause breeders to switch territories in subsequent years but concentrates disturbance to a smaller area. Managers should be aware of the trade-offs in harvesting falcons in the same territories or in different territories in subsequent years. We suggest that resource managers attempt to limit falcon harvest to nestlings from the same territories each year and leave ≥2 nestlings in each nest

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