Management and Conservation Article

Demography of Ferruginous Hawks Breeding in Western Canada

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ABSTRACT We assessed age-dependent survival, site-fidelity, and, together with data on prey and reproduction, trends in the population of ferruginous hawks (*Buteo regalis*) breeding in western Canada. Our analysis included 7,129 ferruginous hawks banded near Hanna, Alberta, and Kindersley-Alsask, Saskatchewan, from 1972 to 2003. We estimated annual adult survival rate to be 0.708 (SE = 0.024) and first year survival for nestlings was 0.545 (SE = 0.147). Resighting probability was modeled as a constant for nestlings (0.009, SE = 0.010), but it varied among years for adults consistent with our sampling efforts. Band reporting rate was at 0.022 (SE = 0.007) for both nestlings and adults. Fidelity to the study site was 1.00 (SE = 0.000) for adults and 0.035 (SE = 0.014) for nestlings. Nesting density ranged from 3.1 to 14.0 pairs/100 km² and averaged 9.8 pairs/100 km². We observed an average clutch size of 3.2 (SE = 0.06) and brood sizes of 2.71 (SE = 0.07) near Hanna and 2.79 (SE = 0.99) at Kindersley-Alsask. Richardson's ground squirrels (*Spermophilus richardsonii*) made up 95% of ferruginous hawk prey. Prey availability was positively correlated with number of offspring near Hanna and Kindersley-Alsask. We believe the lower than expected adult survival did not result in population decrease; rather, declines in reproduction resulting from declines in the abundance of ground squirrels better explain an observed 4.5-fold decline in nesting densities during the study. The results suggest that ferruginous hawk management should address prey in addition to habitat management, and that management needs are regional in scope with particular emphasis on the breeding range within the northern Great Plains. (JOURNAL OF WILDLIFE MANAGEMENT 72(6):1352–1360; 2008)

The ferruginous hawk (*Buteo regalis*) is a large (977–2,074-g) migratory raptor that uses a narrow range of sciurid and lagomorph prey in comparison with other generalist buteos (e.g., Bechard and Schmutz 1995, Giovanni et al. 2007). Several populations of ferruginous hawks have shown gradual and persistent reductions in breeding range, local abundance, and reproduction within their Great Plains and intermountain-basin habitats in western North America (e.g., Woffinden and Murphy 1989, Houston and Schmutz 1999).

Several types of responses by ferruginous hawks to changes in land use or prey have been demonstrated. Some populations have been unable to recover from cyclical declines in prey (Woffinden and Murphy 1989) or vacated local study areas after disease outbreaks among prey in winter (Cully 1991). Conversely, ferruginous hawks showed increased breeding densities and higher reproductive success, responding without delay in the same year when Richardson's ground squirrels (*Spermophilus richardsonii*) rose in abundance (Schmutz and Hungle 1989).

At the landscape level, ferruginous hawks may have vacated close to half of their breeding range on the northern prairies (Houston and Bechard 1984, Schmutz 1984, Houston and Schmutz 1999). Within this prairie range, areas with ≥50% annual crop production are marginally suitable to ferruginous hawks (Schmutz 1987, 1989). This habitat avoidance seems to be mediated by ground squirrels

being more abundant along grassland–field edges than either prevailing cropland or rangeland (Schmutz 1989, Zelenak and Rotella 1997).

In view of such declines, ferruginous hawks are currently listed as "sensitive" by the United States Bureau of Land Management and as a species of concern in several states. The Committee on the Status of Endangered Wildlife in Canada categorized ferruginous hawks as threatened in 1980, vulnerable in 1995, and as threatened again in 2008. Based on what is believed to be a persistent declining trend in Alberta, where much of the species' Canadian range is now located, ferruginous hawks were provincially recognized as endangered in 2006 (Downey 2006).
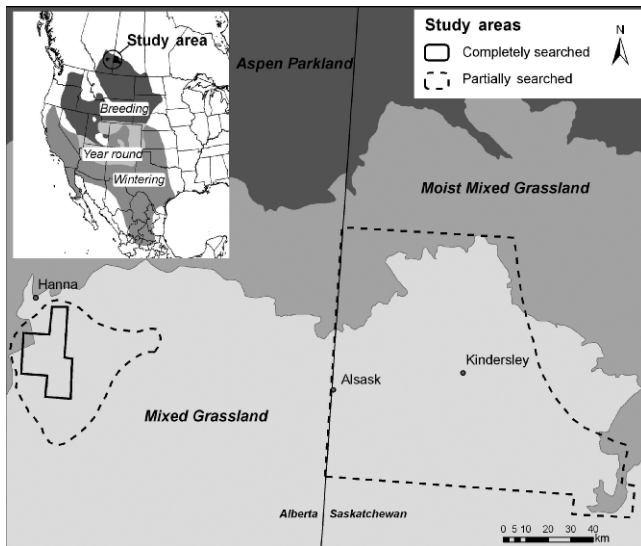
We examined survival and reproduction of ferruginous hawks in response to fluctuations in prey in 2 long-term studies on the northern Great Plains, to evaluate which factor could best explain the species' decline in western Canada.

STUDY AREA

Our study areas near Hanna, Alberta, and Kindersley-Alsask, Saskatchewan, were located in the mixed grass prairie of the northern Great Plains (Fig. 1; Strong and Leggat 1992). Here, ferruginous hawks nested in grasslands and the aspen–parkland edge where the dominant land use was rangeland grazing by cattle at Hanna or grazing and dryland crop production at Kindersley-Alsask.

Some ferruginous hawks nested on sloping or steep ground, but most nested in native or planted trees and

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Figure 1. Study areas near Hanna, Alberta, and at Kindersley-Alsask, Saskatchewan, Canada, in relation to the North American distribution of ferruginous hawks, 1972–2006.

shrubs or artificial nests (Schmutz et al. 1988). Native, drought-adapted grasses (e.g., Thorpe 1999) grew in the gently rolling landscape, with summer temperatures 16.2° C (range 8.7–23.6° C) and rainfall 15.6 cm (range 8.8–23.3 cm = 25th and 75th percentiles; Strong and Leggat 1992).

METHODS

Field Methods

We used banding data (1972–2003) from 3 studies: 2 near Hanna, Alberta (Schmutz et al. 1980, Fyfe and Banasch 1981), and one in the area of Kindersley and Alsask in southwest Saskatchewan (Fig. 1; Houston and Zazelenchuk 2005). We report data on nesting densities and reproduction to 2006.

The study area at Hanna had a variable size but overlapping core area that we searched completely each year using all-terrain vehicles that allowed us to band all surviving nestlings (Appendix). Searching concentrated on areas accessible with automobiles at the Hanna study area's periphery and at Kindersley-Alsask. We marked nestlings during all years of the study, and we captured adults at Hanna from 1975 to 1995 and at Kindersley-Alsask in 1986 (Bloom et al. 1992). We equipped nestlings with alphanumeric color bands at Hanna (1984–1995); these bands were legible with spotting scopes. We assumed that hawks in the 2 study areas 80 km distant were part of the same metapopulation. We obtained recovery data on leg banded hawks from the banding offices of Environment Canada and the United States Geological Survey.

At Hanna, we monitored all potential nest sites during a 10–15–day period in June to obtain a population count and to ascertain reproductive success. For a pair of hawks to be considered nesting, the nest base had to be complete, the cup lined, and the lining flattened as by a hawk's body during laying or incubation. Some nests had been added to and a nest cup completed but not flattened. Presence of

down feathers in the nest material was not a reliable indicator of laying or incubation. Nests in which young had died during the second half of the nestling period generally showed a trampled nest rim, droppings, and a nest cup filled with prey remains and pellets. Nests where young had hatched but soon died showed the original deep cup. Tiny egg fragments from pipped eggs often were lightly buried in the nest cup.

We consistently monitored reproductive success late in the nestling period in both study areas. Because nestling mortality was low at this time, we did not adjust the data based on nestling age and survival probabilities. We excluded broods when brood size was manipulated (e.g., Schmutz et al. 1980) or when nestlings were unusually small (less than half grown) and we could not determine their fate.

We identified all prey to species, sex, and age where possible during visits to nests. We collected pellets on the Hanna study area and examined on site for evidence of ground squirrel, vole or mice, bird, and other remnant prey species. We estimated prey weight using data either from the literature or locally recorded. For ground squirrels, this weight reflected the changing weight of different age and sex groups throughout the season (Schmutz 1977). For whole prey, we assumed the consumable portion to be 85% because the gastrointestinal tract seems not to be consumed (Schmutz et al. 1989), and we assumed the consumable portion proportionately less for various portions of an animal found in nests. Because ground squirrels accounted for 89% of the hawks' food biomass in 1975 and 1976, we focused on ground squirrels to estimate prey availability between years (Schmutz et al. 1980). We calculated an index of ground squirrel abundance between years in 2 ways, via the weight of unconsumed ground squirrels in nests (all 22 yr) and via burrow counts (8 yr).

We counted squirrel burrows showing signs of use (droppings, soil disturbance) within 1 m of a 1-km transect while driving a motorcycle back and forth over study plots. We conducted this count in June during 8 years of the Hanna study on 6 4-ha study plots (see Schmutz et al. 1979). Counts of burrows are variable because they potentially reflected the previous year's burrows not yet collapsed and the extent of dispersal by juveniles. However, these coarse burrow counts should detect large changes in ground squirrel abundance on our study area over time.

Data Analysis

Following Schmutz et al. (2006), we used Burnham's joint resighting–recovery model available in Program MARK to analyze survival (S), resighting probability (p), band-reporting rate (r), and site fidelity (F) of hawks between 1972 and 2003 (Burnham 1993, White and Burnham 1999). Our data set was made up of 2 attribute groups of hawks marked first as adults or as nestlings. Notation follows Schmutz et al. (2006) where a1 indicates no age structure (only one category of age) and a2 refers to age structure with 2 age classes (nestlings and ad). The subscript c-c refers to no time dependence for either age class, t-t refers to full time

Table 1. Best 3 models in descending order used to assess age (*a*) and annual (*t*) or constant (*c*) variation in survival (*S*), resighting (*p*), reporting (*r*), and fidelity (*F*) rates of ferruginous hawks breeding in southern Alberta and Saskatchewan, Canada, 1972–2003. The best-fitting model (A) has the lowest quasi-likelihood Akaike's Information Criterion (QAIC$_c$).[a] We included models A, B, and C in a weighted average for final presentation of results (based on QAIC$_c$ wt [*w*]).

Model[b]	Description	QAIC$_c$	ΔQAIC$_c$[c]	K[d]	*w*[e]	L[f]	Dev[g]
A. $S_{a2 + c\text{-}c}$, $p_{a2 + c\text{-}t}$, $r_{a1 + c}$, $F_{a2 + c\text{-}c}$	Age-related variation in *S*, *p*, and *F*; age-by-temporal variation in ad *p*	2,193.228	0.00	37	0.47	1.00	515.76
B. $S_{a1 + c}$, $p_{a2 + c\text{-}t}$, $r_{a2 + c\text{-}c}$, $F_{a2 + c\text{-}c}$	Age-related variation in *p*, *r*, and *F*; age-by-temporal variation in ad *p*	2,193.851	0.62	37	0.35	0.73	516.38
C. $S_{a2 + c\text{-}c}$, $p_{a2 + c\text{-}t}$, $r_{a2 + c\text{-}c}$, $F_{a2 + c\text{-}c}$	Age-related variation in *S*, *p*, *r*, and *F*; age-by-temporal variation in ad *p*	2,195.186	1.96	38	0.18	0.38	515.69

[a] Variance inflation factor, $\hat{c}$, was 1.471.

[b] *a2* = age-related variation (nestlings and ad), *a1* = no age variation, *t-c* = temporal variation in nestlings only, *c-t* = temporal variation in ad only, *c* refers to constant variation in a given age class.

[c] Difference in value between QAIC$_c$ of the current model vs. the best-fitting model.

[d] *K* = no. of estimable parameters in the model.

[e] QAIC$_c$ wt (likelihood that the current model is the best fitting model from among the 100 tested models).

[f] QAIC$_c$ wt for the model of interest divided by the QAIC$_c$ wt of the best model. This value is the strength of evidence of this model relative to other models in the set of models considered.

[g] Deviance, defined as the difference in −2 log(likelihood) of the current model and −2 log(likelihood) of the saturated model. The saturated model is the model with *K* equal to the sample size.

dependence for both age classes, and *t-c* or *c-t* indicates time dependence for nestlings only or adults only, respectively.

We identified a priori a limited number of models that were fully age and time dependent with respect to *S* and *p* but only age-related variation in *r* and *F* because band recoveries were limited (e.g., Arnold et al. 2002, Schmutz et al. 2006). We first constructed our global model ($S_{a2 + t\text{-}t}$, $p_{a2 + t\text{-}t}$, $r_{a2 + c\text{-}c}$, and $F_{a2 + c\text{-}c}$) and applied the parametric bootstrap with 1,000 simulations to estimate the variance inflation factor ($\hat{c}$), calculated as the deviance estimate for our actual data divided by the average simulated deviance (Burnham and Anderson 2002, Cooch and White 2007). We progressed with model building by reducing age and time dependency parameterization until we reached our simplest model ($S_{a1 + c}$, $p_{a1 + c}$, $r_{a1 + c}$, and $F_{a1 + c}$). Age structured parameter estimates for individuals marked as nestlings included only the first year of life and thus the age category "adult" included all birds aged ≥1 years (i.e., subad and ad; Schmutz et al. 2006). We did not consider gender in any of our models because we could not accurately sex all nestlings, captures were limited, and we did not expect large differences in survival between sexes as in other raptor species (e.g., Bowman et al. 1995, Lieske et al. 2000).
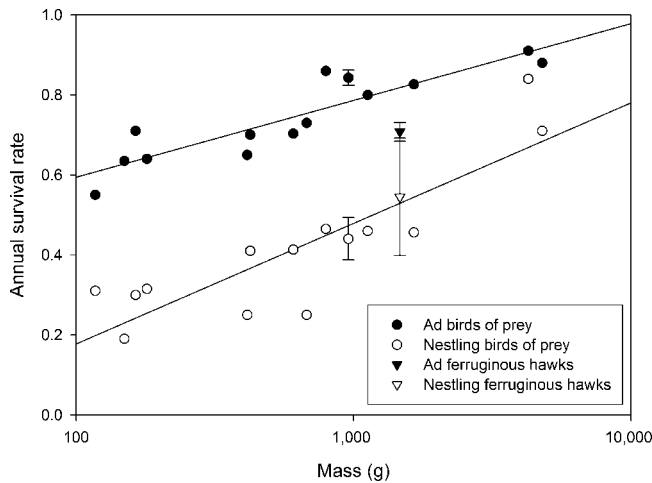
We selected the best approximating model using Akaike's Information Criterion (AIC) adjusted for small sample sizes and overdispersion (QAIC$_c$; Burnham and Anderson 2002). Information-theoretic techniques promote the simplest model that explains the greatest variation in the data, and thus our limited band recoveries and resightings was taken into account during model selection. We ranked the model with the lowest QAIC$_c$ as best and used differences in QAIC$_c$ between that model and all other models (ΔQAIC$_c$) to identify those that held support. We calculated the ΔQAIC$_c$ weight for each candidate model; these weights sum to 1.0 and represent the relative likelihood of each model (Burnham and Anderson 2002). We used model averaging, weighted according to ΔQAIC$_c$, to present parameter estimates (Burnham and Anderson 2002).

We compiled survival estimates of adult and juvenile (≤1-yr) birds of prey of 15 species to plot the expected relationship between survival and mass (Haug et al. 1993, Preston and Beane 1993, Rosenfield Bielefeldt 1993, Sodhi et al. 1993, Crocoll 1994, Gehlbach 1995, MacWhirter and Bildstein 1996, Steenhof 1998, Buehler 2000, Kochert et al. 2002, Poole et al. 2002, Smallwood and Bird 2002, White et al. 2002, Kauffman et al. 2003, Schmutz et al. 2006). Because birds of prey are commonly dimorphic, we used the mean mass of adult males and females. We then added results from this study, including variance, to determine whether adult or nestling ferruginous hawks showed higher or lower than expected survival rates. We used Pearson correlations to plot the expected relationship between survival of adults and nestlings. Finally, we estimated lambda from breeding densities and bootstrapped variance about the annual, geometric mean of lambda (λ; Manly 1997).

RESULTS

We banded 115 adult and 6,687 nestling ferruginous hawks, yielding 158 band recoveries (age when reported: ad = 33, nestling = 125) and 169 adult resightings (36 of 70 resighted individuals were marked as nestlings; however, all resightings were of birds ≥1 yr old and thus considered ad). After adjusting our $\hat{c}$ = 1.47, our best-fitting model ($S_{a2 + c\text{-}c}$, $p_{a2 + c\text{-}t}$, $r_{a1 + c}$, $F_{a2 + c\text{-}c}$) specified age-related variation in survival and fidelity and age-by-temporal variation in adult resighting probability (Table 1). Only 2 other models were comparable with the top model (ΔQAIC < 2) to be included in a model average: 1) a model that indicates no age-dependent survival differences but age-dependent recovery rates of dead birds and 2) a model identical to the best-fitting model but with age-related variation in reporting rate (Table 1). Both adult (0.708, SE = 0.024) and

Figure 2. Mass and annual survival estimates for some adult and nestling (<1-yr) birds of prey that breed in North America. Data points with error bars (±1 SE) are for the lighter Swainson's hawk (Schmutz et al. 2006) and the heavier ferruginous hawk (triangles; this study) from the same study areas.

nestling (0.545, SE = 0.147) annual survival was best modeled as a constant through time. Resighting probability was modeled as a constant for nestlings (0.009, SE = 0.010) but varied among years for adults, which was consistent with our sampling efforts. Program MARK yielded a 2.2% probability that a dead ferruginous hawk would have its band reported in any one year, which did not differ between nestlings and adults (0.022, SE = 0.007). We estimated fidelity as 1.00 (SE = 0.000) for adults and 0.035 (SE = 0.014) for nestlings.

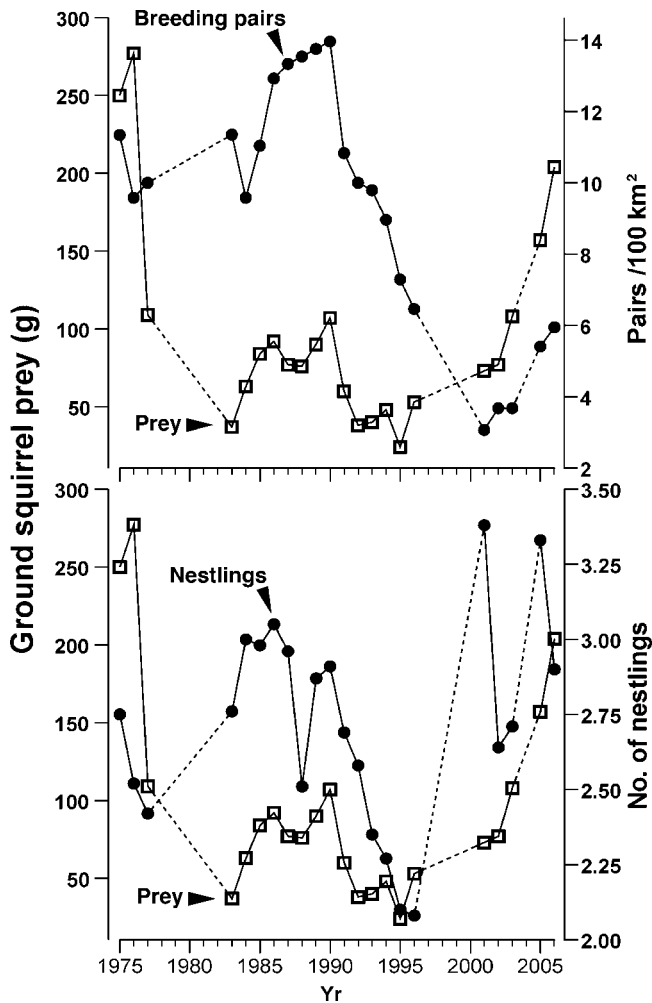We determined annual nestling and adult survival for 15 species of raptors (Fig. 2). Survival rates correlated between adults and nestlings ($r = 0.767$, $P = 0.001$, $n = 15$) with adult survival higher ($r = 0.734$, $P = 0.002$, $n = 15$) than that of nestlings ($r = 0.900$, $P < 0.001$, $n = 15$) with respect to mass. Adult ferruginous hawk survival fell outside the scatter plot for other raptors and was thus lower than expected (Fig. 2).

To place survival in the context of broader population dynamics, we examined changes in nesting densities and reproduction and attempted to relate these to availability of prey. The number of nesting pairs at Hanna, Alberta, showed a 4.5-fold decline from a high of 13.96 pairs/100 km² in 1990 to a low of 3.07 pairs/100 km² in 2001 (Table 2; Appendix). We estimated the geometric mean of the finite rate of increase of the population (λ) from 1976 to 2006 as 0.970 (95% CI = 0.884–1.062). Annual variation in reproductive success was similar between Hanna and Kindersley-Alsask (Figs. 3, 4). The proportion of breeding pairs that were able to raise young at least close to fledging ranged from 51% to 92% annually at Hanna (Appendix). Average number of nestlings near fledging in late June to early July varied significantly in both study areas over the study period (Table 2). Fledgling number ranged from 2.08 in 1996 to 3.38 in 2001, with an overall average of 2.71 at Hanna (Appendix) and from 2.24 in 1996 to 3.38 in 1976, with an average of 2.82 at Kindersley-Alsask (Houston and Zazelenchuk 2005).

Ferruginous hawks fed primarily on ground squirrels (Table 2). During 1,201 visits to nests at Hanna between 1975 and 2006, an estimated 129 kg of whole or partial prey items found included 95.0% Richardson's ground squirrels, 0.5% thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), 2.0% birds, 1.9% hares, 0.1% mice or voles, and 0.4% other mammals and a frog. An analysis of 233

Table 2. Changes in ferruginous hawk nesting density, amount of squirrel prey per visit to nests, number of visits and number of ferruginous hawk nestlings near Hanna, Alberta, and Kindersley-Alsask, Saskatchewan, Canada, from 1975 to 2006. We grouped years with consistency in these demographics into 5 separate periods to illustrate the change between them. We did not record nest densities in Saskatchewan.
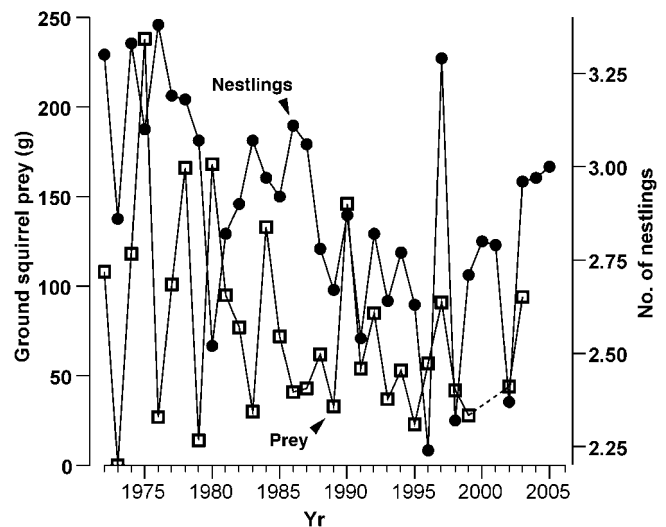
Period	Breeding pairs/100 km²		Estimated mass of ground squirrel prey/visit			No. of nestlings	
	No.	SE	Mass (g)	SE	No. of visits	$\bar{x}$	SE
Hanna							
1975–1977	10.3	0.5	198	18	281	2.56	0.10
1983–1985	10.7	0.6	72	9	165	2.91	0.08
1986–1990	13.5	0.2	88	6	407	2.86	0.09
1991–1996	8.9	0.7	46	5	262	2.34	0.10
2001–2006	4.4	0.6	124	19	67	2.99	0.15
Total	9.3	0.7	104	5	1,182	2.72	0.07
Test	$\phi = 0.636$		G = 58.52			G = 0.86	
df	1		12			12	
P	0.009		<0.001			<0.001	
Kindersley-Alsask							
1975–1977			124	64	34	3.21	0.95
1983–1985			79	16	104	2.98	0.97
1986–1990			67	9	229	2.84	0.98
1991–1996			50	6	331	2.61	0.96
2001–2006			70	13	102	2.78	1.00
Total			64	5	800	2.79	0.99
Test			G = 14.97			G = 24.67	
df			12			12	
P			0.243			0.017	

Figure 3. Relationships between estimated amount of consumable ground squirrel prey in ferruginous hawk nests, and nesting density (top) and number of nestlings per nest (bottom) at Hanna, Alberta, Canada, 1975–2006.

Figure 4. Relationship between estimated amount of consumable ground squirrel prey (triangles) and nestling ferruginous hawks (squares) at Kindersley-Alsask, Saskatchewan, Canada, 1972–2005.

0.036). In general, we found that the amount of squirrel prey available varied significantly at Hanna over time, but not at Kindersley-Alsask, despite a declining temporal trend (Table 2). Squirrel availability corresponded closely with reproductive success within and between study areas but not with nesting density monitored at Hanna (Table 3).

Annual variation in prey availability corresponded to variation in number of nestlings (Figs. 3, 4). The decline in ground squirrels evident on the Hanna study area (Fig. 3; Table 2) was verified by 2 indices independent of prey counts at nests. First, using poison data (strychnine) as an independent and region-wide index of ground squirrels in spring, Schmutz and Hungle (1989) showed a strong correlation between poison sales and nesting densities of ferruginous hawks ($r_s = 0.658$, $P = 0.031$). Poison sales in the region, including Hanna, had tripled in the years when unprecedented numbers of ground squirrels were evident on the study area. This rise in ground squirrels corresponds temporally to a rise in number of nestlings and nesting densities, and it corroborates a rise in prey at nests (Fig. 3).

A second index of ground squirrel abundance showed a decline in ground squirrels on the Hanna study area, and it corroborates the decline in amounts of prey in nests during the 1990s and early 2000s in comparison with the 1970s. On the 6 4-ha study plots at Hanna, 111 adult males and females were present in spring in 1975, and 77 in 1976, before the emergence of young (Schmutz et al. 1979). The average number of burrows counted on these 6 plots on 1-km transects each June were 11.7 in 1975, 31.3 in 1976, 0 in 1996, 1.8 in 2001, 0 in 2002, 0.2 in 2003, 2.3 in 2005, and 0.5 in 2006. Changes in burrows counted during these 8 years were correlated with the corresponding estimates of prey remains ($r_s = 0.792$, $P = 0.036$).

Given the near complete reliance on ground squirrels, we plotted changes in prey availability with nesting densities and the number of nestlings reared to near fledging. We detected prey availability variation and reproductive success

pellets examined at nests contained remains of ground squirrels (90%); mouse or vole remains (<1%); feathers (<1%); and ground squirrel, hare, mouse or voles, and feathers in various combinations (8%). For comparison, pellets combined with prey items found during daily visits in 1975–1976 yielded 89% ground squirrels, 3% mice or voles, 2% hares, and 6% birds (Schmutz et al. 1980). In Saskatchewan, 74 kg of whole or partial prey items found included 95.7% Richardson's ground squirrels, 0.6% thirteen-lined ground squirrels, 1.3% birds, 0.9% hares and rabbits, 0.9% mice and voles, and 0.6% other mammals.

Because of the prevalence of ground squirrels in the ferruginous hawk's diet and to allow for greater specificity in our management recommendations, we consider only ground squirrel prey in our subsequent analyses. We assumed that the amount of ground squirrel prey found in nests reflected its availability to the pair in their nesting area and collectively in the study area. To test this assumption, we correlated the 8-year burrow counts with prey remains and we found a significant relationship ($r_s = 0.792$, $P =$

Table 3. Meta-analysis of ferruginous hawk population trends near Hanna, Alberta, and Kindersley-Alsask, Saskatchewan, Canada, 1983–2006. We used Spearman rank correlations to rank the strengths in relationships between population parameters within and between study areas.

	Hanna			Kindersley-Alsask	
	Breeding pairs/100 km²	No. of nestlings	% nests with ≥1 young	Prey	No. of nestlings
Hanna					
Prey	−0.015***	0.598*	0.357**	0.411**	0.377**
Nests/100 km²		0.044***	−0.023***	−0.037***	0.279***
No. of nestlings			0.334***	0.212***	0.701*
% nests with young				0.267***	0.277***
Kindersley-Alsask					
Prey					0.298***

* $P < 0.05$, ** $P = 0.051$–0.150, *** $P > 0.150$.

changes that were similar between Hanna and Kindersley-Alsask that resulted in similar population changes (Figs. 3, 4). In 1975–1977, prey was apparently abundant, yet nesting densities and number of nestlings were moderate. A decline in prey (1983–1985) did not change nesting densities, but brood size increased at Hanna and decreased at Kindersley-Alsask to similar levels between the 2 areas. Moderate prey availability in 1986–1990 corresponded with high nesting densities but no increase in brood size. The years of population decline (1991–1996) were also the years with lowest amounts of prey at nests and lowest reproductive output both at Hanna and Kindersley-Alsask. A recent rise in prey corresponded with a recovery in densities (2001–2006), but this recovery was slow (Table 2).

DISCUSSION

Life-history theory suggests that large birds of prey should have high survival and low fecundity relative to smaller birds of prey (Sæther 1989). Adult survival below this expected rate may indicate a population with the potential to decrease, whereas higher than expected juvenile survival may indicate increased potential for recruitment. Compared with the expected relationship between survival of adults and nestlings (<1 yr), ferruginous hawk adults had lower than expected survival whereas estimates for nestlings were on par with expectation (Fig. 2). Woffinden and Murphy (1989) estimated the survival of adults based on nest re-occupancy rates as 75%, which was slightly higher than our observation of 71%. First-year survival of ferruginous hawks after fledging has been previously estimated at 34% (Schmutz and Fyfe 1987) and may be an underestimate because most reported hawks were the result of human-caused mortality (e.g., shootings and vehicle collisions; Bechard and Schmutz 1995). Our estimate (54%) was substantially higher possibly because of a large sample of recoveries and the ability to resight philopatric hawks returning to natal areas the year after fledging.

Our results do not suggest that fluctuations in breeding densities were caused by variable annual adult mortality. Rather, we document periods of prey fluctuations that tend to match breeding success of hawks across 2 study areas (Table 2), which is consistent with other studies of raptors where food has been identified as the single-most important

factor affecting the dynamics of species (Newton 1979). However, despite an exceptionally high (95%) reliance on one species as prey (Richardson's ground squirrels), ferruginous hawks' responses to changes in prey were complex.

One instructive anomaly in the prey and hawk density relationship was the rapid rise in nesting density during 1986–1990, contrasted with a slow rise in 2001–2006. Over a mere 2 years from 1984 to 1986, the hawk population at Hanna grew rapidly from moderate to high densities (Appendix), an increase of 34% (Fig. 3). In contrast, the hawk population after 2000 responded only slowly. Prey availability as measured at nests had reached moderate to high levels by 2001, and reproduction had also recovered. In other areas, Woffinden and Murphy (1989) showed in a long-term study that a population of ferruginous hawks became nearly extirpated in Utah in synchrony with a black-tailed jackrabbit (*Lepus californicus*) population decline. Woffinden and Murphy (1989) noted, however, that when the hare population increased, the hawks did not, which is similar to our study in the sense that prey at nests and brood size increased substantially at Hanna during 2001–2006, yet nesting pairs changed little in 2001–2003 and rose only slowly by 2005–2006. This slow response seems different from the rapid response under already moderate densities in the 1970s and early 1980s.

Our joint resighting–recovery model estimated the hawks' study area fidelity as 1.0 for adults and 0.035 for nestlings. It is possible that after a decade of low prey in the 1990s, many former territory residents had died and due to low reproduction a sufficient surplus of hawks able to breed was not available for a rapid and complete recovery. Furthermore, the pairs and nesting areas involved in the population recovery tended to include long-held nesting areas. We speculate that above average individual or territory quality was influential first in the persistence of pairs during prey-poor years, and second, in the subsequent population recovery. Such high-quality pairs or territories may have been limited. This is consistent with the observation that the 13 nests in use during ≥1 early recovery years from 2001 to 2003 showed a long-term occupancy of 5–18 years ($\bar{x} = 12.9$) in the 22-year study.

In the meta-comparison across study areas and factors, low

correlations with nesting densities at Hanna are noteworthy. Territory fidelity is high in this species (J. K. Schmutz, University of Saskatchewan, unpublished data) and could act as a buffer to changing conditions in a subsequent year, which suggests that separate analyses based on individual years, and between periods, are warranted. Low correlations between nesting densities and other factors, particularly prey at nests, may also arise if these track different points in the annual cycle of prey species. For example, both overwinter survival of squirrels (abundance in early spring) and litter size (added in early summer) determine the sum-total of prey abundances in the hawks' reproductive cycle. These 2 temporally separated changes in prey availability probably require separate interpretation. When squirrel survival over winter is low, some hawks may not settle to breed, which is consistent with the observation that some nests even in long-term territories had been attended to but were not completed (Appendix). We do not believe these to be simply alternate nests because in some cases pairs or individual hawks were present and because their distance from other nests resembled normal internest distances. Squirrel overwinter survival alone most likely influences both the number of hawks settling in spring and their clutch size, whereas the litter size of squirrels may influence the hawks' brood rearing success.

Ferruginous hawk densities recorded at Hanna are among the highest reported for this species (Bechard and Schmutz 1995). However, we still believe that the trends reported here are representative of this species generally. High densities at Hanna were likely due in part to the favorable ratio of grassland (approx. 80%) to cultivated land (e.g., Schmutz 1989, Zelenak and Rotella 1997). An additional factor may be the comparatively mesic conditions and higher ecosystem productivity in comparison with what this arid-country raptor might encounter in some other areas within its range. Still, densities at Hanna are comparable with raptors of similar size (Newton 1979). Furthermore, in Saskatchewan, where nests were widely distributed including across intensively used agricultural landscapes, trends in prey use, prey availability, and brood size were similar.

Woffinden and Murphy (1989) attributed the absence of an expected rise in density to low reproduction and nomadism. Large scale nomadism in the sense of Hunter (1995) has not been described for ferruginous hawks. Based on our data, our model suggests that survival was constant throughout the population highs and lows in the study period and site fidelity was high. Our data are consistent with the low-reproduction interpretation, which, coupled with a survival rate that is slightly below average considering the ferruginous hawk's body size, suggests that a non-breeding segment able to respond rapidly to local increases in prey was small or nonexistent.

The largely unexplained decline in prey on both study areas in the 1970s may have been influenced by climate, which may be important for conservation. Data indicate that hatch date among ferruginous hawks, but not Swainson's hawks (*B. swainsoni*), varies in accordance with the emergence of young ground squirrels (Schmutz et al. 1980). Since the 1970s, spring now occurs earlier (e.g., Beaubien and Freeland 2000), and field observations suggest that ground squirrels emerge earlier. Ecological costs associated with mismatched timing events are being recognized, which may be particularly significant for both migrants and hibernating mammals (Inouye et al. 2000, Thomas et al. 2001).

MANAGEMENT IMPLICATIONS

The ferruginous hawk's low survival in relation to other adult raptors implies that mortality factors such as collisions and electrocution remain important, but that mortality factors specifically affecting adults (e.g., breeding territorial strife) may also be important. The high densities and reproductive output of ferruginous hawks here suggest that the northern Great Plains remain important for regional conservation planning. Similarly, a possible negative impact of climate change on hibernating sciurids implies that a possible shift in breeding- and winter-range toward northern latitudes and higher elevation could be expected.

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Appendix. We show the size of the defined study area, number of ferruginous hawk nests monitored, reproduction outcomes, and number of young raised to fledging per year for the Hanna, Alberta, Canada, study area (1975–2006). We counted a breeding pair when nests were at least completed with nest lining flattened, or when nests contained eggs or young. Off-area nests were outside of the defined and completely searched core area.

Yr	Study area (km²)	Incom-plete nests	Completed nests	Pairs/ 100 km²	λ	Outcome known	Nest fell	Abandoned Before hatch	Abandoned After hatch	Abandoned Stage unknown	Nests with ≥1 young	$\bar{x}$	SD	Nests with brood size known	Off-area nests
1975	335	1	38	11.34		37	1	6	2	0	28	2.75	0.99	24	1
1976	480	4	46	9.58	0.845	41	3	6	11	0	21	2.52	1.17	21	6
1977	480	1	48	10.00	1.044	47	1	5	5	3	33	2.42	1.06	31	14
1983	326	3	37	11.35	1.135	36	1	1	4	1	29	2.76	1.17	25	0
1984	480	7	46	9.58	0.844	45	0	4	2	0	39	3.00	0.87	38	47
1985	480	2	53	11.04	1.152	48	0	2	4	1	41	2.98	0.96	41	58
1986	480	3	62	12.92	1.170	62	0	3	2	2	55	3.05	1.02	54	68
1987	480	2	64	13.33	1.032	64	1	3	3	3	54	2.96	1.03	54	51
1988	480	1	65	13.54	1.016	63	1	2	4	2	54	2.51	0.99	53	27
1989	480	0	66	13.75	1.016	66	0	5	7	1	53	2.87	0.90	53	20
1990	480	0	67	13.96	1.015	67	1	4	3	3	56	2.91	1.07	56	22
1991	480	1	52	10.83	0.776	50	0	1	2	5	42	2.69	1.05	42	33
1992	480	1	48	10.00	0.923	46	0	3	3	0	40	2.58	1.07	38	15
1993	480	2	47	9.79	0.979	46	1	1	5	5	34	2.35	0.81	34	24
1994	480	1	43	8.96	0.915	43	1	2	2	1	37	2.27	0.77	37	27
1995	480	1	35	7.29	0.814	34	0	6	8	0	20	2.10	0.91	20	15
1996	480	2	31	6.46	0.886	31	0	2	3	2	24	2.08	1.06	24	13
2001	326	2	10	3.07	0.475	10	0	1	1	0	8	3.38	0.52	8	12
2002	326	0	12	3.68	1.199	12	0	0	1	0	11	2.64	0.81	11	13
2003	326	5	12	3.68	1.000	12	0	1	3	1	7	2.71	0.76	7	10
2005	185	1	10	5.41	1.470	10	0	0	0	1	9	3.33	0.71	9	1
2006	185	1	11	5.95	1.100	11	0	1	0	0	10	2.90	0.74	10	8
Total		41	903	9.81	0.970	881	11	59	75	31	705	2.71	0.99	690	485