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Rapid Sustainability Modeling for Raptors by Radiotagging and DNA-Fingerprinting

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ABSTRACT Sustainable use of wildlife is crucial to ensuring persistence of natural resources. We used age-specific survival and breeding data to parameterize a demographic model for a harvested Kazakh saker falcon (*Falco cherrug*) population by radiotagging juveniles and estimating adult turnover with DNA-fingerprinting during 1993–1997. We gathered similar data during 1990–1998 to model populations of British buzzards (*Buteo buteo*), and during 1980–1998 to model populations of Swedish goshawks (*Accipiter gentilis*). Leg-bands and implanted microtransponders provided ways to test for bias and to estimate the harvest of sakers for falconry. Despite an estimated minimum first-year survival of only 23%, the observed productivity of 3.14 young per clutch would sustain a saker population (i.e., $\lambda = 1$) with a breeding rate (at laying) of only 0.63 for adults or with a residual juvenile yield of 37% if all adults breed. Higher first-year survival rates for goshawks and buzzards correlated with juvenile yields of up to 71%, but no more than half as many individuals if adults also were harvested. An annual population decline of 40% for sakers in southern Kazakhstan could be explained by observed productivity of only 0.71 young per clutch if there was also an estimated harvest of 55% of adults. This study shows that demographic models such as these can now be built rapidly if nestlings are fitted with reliable and safe radiotags and adult turnover is estimated from genetic analyses or other techniques. (JOURNAL OF WILDLIFE MANAGEMENT 71(1):238–245; 2007)

The sustainable use principle, as defined in the Convention on Biological Diversity, is not only a safeguard for harvested wildlife, but it also can motivate habitat conservation that maintains biodiversity in general (Geist 1994, Freese 1998). However, to ensure that use is genuinely sustainable, it is important to have models that predict how populations respond to harvest (Beddington and May 1977, Rosenberg et al. 1993). If data for modeling can be collected at minimal cost, then human resources are released for other conservation tasks.

Models to predict population change require data on productivity and age-specific survival rates. Productivity can be recorded by visiting nests, and survival rates of birds have traditionally been estimated by banding (Greenwood et al. 1978). Turnover of breeding adults can be estimated through trapping at nests, followed by recapture or resighting of marked individuals (Cade 1960, Mearns and Newton 1984, Tordoff and Redig 1997), or in some species by recognition of patterns on molted feathers (Opdam and Müskens 1976, Rust and Kechele 1996). Alternatively, collection of blood, feathers, or other genetic samples at nests without trapping requires less effort, avoids risk of

capture bias, and allows more objective assessment than most other techniques.

Survival of individuals from fledging to breeding can be estimated by banding, but the necessary precision requires marking several hundred birds, coupled with long-term band-return programs. This may be impractical for rare species or in areas with few interested observers. Moreover, age-specific recovery bias (Anderson et al. 1985) is especially likely to affect survival estimates for juveniles in raptor studies (Lakhani and Newton 1983). Radiotagging is an alternative to banding for estimating survival rates but requires tests that tagging itself does not bias the data (White and Garrott 1990).

During 3 consecutive studies of radiotagged raptors, we progressively eliminated sources of bias and reduced the time needed to build sustainability models. The 18 years required for the first study, on northern goshawks (*Accipiter gentilis*) in Sweden, was reduced to 4 years of data collection for the last study, of saker falcons (*Falco cherrug*) in Kazakhstan. The rapid modeling depended on combining a reliable design of radiotag, which gave a maximal 7% annual failure rate in a second study, of common buzzards (*Buteo buteo*) in southern England (Kenward et al. 2000), with DNA-fingerprinting for wildlife (Wetton et al. 1987,

Burke et al. 1989, Gibbs et al. 1990, DeWoody 2005) to estimate turnover and survivorship.

Rapid modeling was important because sakers, which breed in Eurasia from Austria to Manchuria (Cramp and Simmons 1980), are an important wildlife resource. For centuries they have been trapped on autumn migration to Africa and the Indian subcontinent for use by falconers in the Middle East through the winter before being released in spring (Allen 1982). However, dissolution of the Soviet Union gave access to saker breeding areas, raising concern that high market values would increase harvest levels from the estimated 2,750 falcons obtained annually in the late 1980s (Riddle and Remple 1994). To check that harvests were sustainable, our 4 years of breeding and survival data included tests from band and microtransponder recoveries for adverse impact of radiotags. We show how population structures based on an age-specific survival and breeding (ASSAB) model differed between goshawks, buzzards, and sakers, but that in all cases appreciable proportions of adults were nonbreeding. We use a model parameterized with data from northern Kazakhstan to estimate sustainable yields and to investigate a severe decline of the saker population in southern Kazakhstan.

STUDY AREA

We equipped goshawks with bands and tail-mounted radiotags during 1980–1987 on the 3,100 km^2 Swedish island of Gotland, which extends approximately 120 km north–south, up to 35 km east–west and is 90 km from the nearest mainland in the Baltic sea (details in Kenward et al. 1999). We fitted buzzards with bands and backpack radios during 1990–1998 on the south coast of England and radiotracked them to a northward radius of 100 km on roads and up to 350 km in aircraft, to include Wales and East Anglia (details in Walls and Kenward 1998, Kenward et al. 2000).

We attached bands and backpack radios to 61 nestling sakers during 1993–1995 in northern Kazakhstan. We also recorded productivity at cliff nests in study areas in southeast Kazakhstan, where in 1993–1994 we tracked to dispersal another 28 sakers that we radiotagged as fledglings. This southern population, for which harsh terrain prevented monitoring beyond dispersal, is considered to be sedentary (like the buzzards in Britain and goshawks on Gotland) and the 2 studied subpopulations on cliffs 300 km apart were separated by similar distances from other populations (Pfeffer 1986).

METHODS

In our first study, we used exclusively tail-mount transmitters, which were shed by goshawks at molt and had a high failure rate. It took 18 years of study, starting in 1980, to check effectively for bias from possible adverse effects of 1) radios on the hawks, 2) trapping of adults, and 3) loss of signals due to death of batteries and hawks. By 1998 we had adequate numbers of band recoveries to compare survival of telemetered hawks with those marked only with bands

Table 1. The number of saker falcons marked and the number subsequently reported trapped the following autumn at study areas in northwest and southeast Kazakhstan during 1993–1995.

Marking combinations	South	North	Total	Trapped
Bands + microtransponders + radios	28	61	89	7
Bands + microtransponders	17	65	82	6
Total	45	126	171	13

(Kenward et al. 1999). The bias-corrected estimate of adult survival rate of 83% was similar to estimates from banding, but first-year survival rates of 49% for males and 71% for females (58% combined) were apparently unbiased and were higher than 38% from contemporary band recoveries (Kenward et al. 1999).

In the second study, we mounted backpack radios that transmitted for 2–4 years on buzzard nestlings, thus avoiding capture-based bias by tagging all the young in an area as nestlings. Tests in the first 2 years of study showed that survival and behavior of birds with backpacks was the same as others with tail-mounted tags (Kenward et al. 2000). Premature loss of tag signals was infrequent (7% in the first yr) and almost exclusively on known emigrants. We treated lost tags as deaths because all known distant emigrants with functioning radios were recorded making philopatric visits in spring (Walls and Kenward 1998). On this basis, the (min.) 88% adult survival was the same as for band recoveries, and the first-year survival of 66% was again higher than 55% from contemporary band recoveries, without differences between sexes (Kenward et al. 2000).

We fitted backpack radios with a life of 2 years, a weight of 22 g, and a 40-km range on 61 saker falcon nestlings (Table 1; Biotrack Ltd., Wareham, United Kingdom) in northern Kazakhstan. We checked survival every 3–5 days before dispersal from nest areas. From late March to late April in the natal area of northern Kazakhstan, we sought radio signals of falcons fledged in the 2 previous years (until 1997) with an automated system and with independent checks using handheld receiving equipment at 2–3 day intervals. We recorded productivity by visiting nests in April to record presence of pairs with eggs, because egg laying was an objective criterion for a breeding attempt in our models, and again in May to check whether young had hatched. We estimated the age of young from wing length, and a final visit allowed sex identification (Kenward et al. 2001) and marking just before fledglings left the nest. We used bands alone to mark 17 southern young (Table 1), including 5 young that we opportunistically marked just outside the area of historical occupancy that we regularly searched.

We also marked the 171 banded falcons, including the 89 with radios (Table 1), with 2×13 mm microtransponders (Avid, Norco, CA). We injected microtransponders subcutaneously to lie at the posterior end of the keel. We reported bands on falcons trapped in autumn through the British Trust for Ornithology, and transponders were detected at veterinary hospitals in the Middle East where these markers were used routinely to identify trained falcons.

We drew blood by syringe from a brachial vein for genetic

analysis of young in the north. We stored 10 drops of blood in ethanol on ice in 1.5-mL Eppendorf tubes. Following the protocols of Sambrook et al. (1989) and Swatschek et al. (1993, 1994), we performed DNA isolation, including digestion by restriction enzymes (HinfI), agarose electrophoresis, and capillary transfer to a nylon membrane (Biodyne B; Pall GmbH, Dreieich, Germany). After prehybridization, we incubated nylon membranes in a hybridization mixture containing 10 pmol/mL of digoxigenated oligonucleotide probe (GGAT)[4] (Fresenius AD, Bad Honburg, Germany) to detect minisatellites. We marked DNA or DNA-hybrids by an antibody that was raised against digoxigenin (Boehringer; Roche Diagnostics, Mannheim, Germany). This antibody was coupled to a phosphatase that in turn produced a colored precipitate at the sites of hybridization (Wink et al. 1999).

We calculated band-sharing coefficients (BSCs) for saker broods as $(C \times 2)/(A + B)$, where A and B are the total number of bands in the DNA profiles of individuals A and B, and C is the number of shared bands (Jeffreys et al. 1985). We compared BSCs between broods with Mann–Whitney U tests to estimate turnover of adult parents at nests.

Age-specific survival and breeding models used the equation

$$n_{j,k,0} = \sum_{x=1}^{\omega} b_{k,x} \times y_{k,x} \times n_{j-x,k,0} \prod_{i=1}^{x} s_{k,i},$$

where $n_{j,k,0}$ is the number of young of sex k produced in year j, $b_{k,x}$ and $y_{k,x}$ are the sex-specific breeding rate and productivity of breeders at age x, $n_{j-x,k,0}$ is the number of young produced x years before year j, $s_{k,i}$ is the sex-specific survival, and ω is the maximum breeding age (Kenward et al. 1999). We used the ASSAB models to estimate yields as proportions of different age groups that could be removed sustainably from balanced (no-growth) populations in which $n_{j,k,0} = n_{j-x,k,0}$. Comparative data on survival and breeding of goshawks and buzzards are from Kenward et al. (1999, 2000). We applied juvenile survival rates until 31 March of the year following hatching and adult rates thereafter.

RESULTS

Survival Estimates for Juveniles
Of the 89 radiotagged saker falcons, 81 (91%) survived the 20–45 days between leaving the nest and dispersal from natal areas in July and early August. The other 8 young falcons were killed by predators (6 cases) or disappeared shortly after fledging (2 cases). We detected signals in the northern study area in first or second springs after fledging for 5 (2 F, 3 M) of 23 northern young from 1993, 6 (6 F, 0 M) of 23 from 1994, and 3 (2 F, 1 M) of 15 from 1995. Minimum first-year survival rate was 14 of 61 young (23%, binomial SE ±5%).

We obtained records from trapping for 7 of the 89 radiotagged falcons (8%, ±3%), and 6 of 82 birds without radiotags (7%, ±3%) during or after their first September. The comparable rates of recovery ≥2 months after fledging

suggested that radiotagged and other birds survived at a similar rate for ≥1 month of independence from their parents. The 13 records of trapped falcons (10 F, 3 M) included 10 band returns and 4 transponders detected in falcon hospitals (with one transponder record from Abu Dhabi for a falcon from which the band had been removed and reported 3 months previously in Syria). From the northern study area, 8 recoveries represented 6% of 126 marked sakers. From the southern study area, 5 recoveries were 11% of the 45 young that we marked.

Turnover and Productivity of Adults
We calculated at least 3 BSCs across intervals of 1–3 years for 34 broods of young saker falcons in 14 breeding territories. We compared these between-year BSCs 1) with ≥3 within-year BSCs, which indicated sibling relatedness in each territory, and 2) with a mean of 0.19 (±0.01; range = 0.10–0.33) for 70 BSCs between young in different territories, which provided a value for unrelated birds. We obtained 3 patterns of relatedness across years for broods from the same territory:

1. no difference in BSCs among years indicated that broods were full sibs across years,
2. between-year BSCs between those for full sibs and those for unrelated broods, and
3. between-year BSCs did not differ from those for unrelated broods.

For estimating adult turnover, these indicated 1) no change of parents, 2) change of one parent, and 3) change of both parents. The data (Table 2) indicated the loss of 10 adults from breeding territories across 28 pair-years (i.e., 56 yr). With the assumptions that each loss represents death of an adult and that survival remained constant across years, adult survival was 82% (±5%). We found no evidence from bands that adults lost from one nest bred subsequently at another, but one of the 99 young birds in the 34 broods contained an anomalous band that probably indicated an extra-pair copulation.

Productivity remained high during the 4 years study in the north (Table 3), with 198 young from 63 clutches giving 3.14 young per clutch. No falcons bred as 1-year-olds in the north. We identified robbing of nests by reports from local people and sign of human presence (e.g., tire tracks when young disappeared). These thefts reduced productivity and in 1996 all young were taken from the 3 of 21 checked nests that remained occupied in the south. In 1993–1994, 3 of 16 females breeding in the south were 1-year-olds (we could not check this at 8 of the 24 nests), and 2 of 11 were 1-year-olds in subsequent years, which suggested an insufficiency of adults to fill vacancies (Bragin 1986, Balbontin et al. 2003).

Sustainability Models and Harvest Estimates
Age-specific survival and breeding models of age structure in breeding populations (on 1 Apr) show that the saker falcon population that we studied contrasted strongly with populations of buzzards and goshawks (Fig. 1). The low first-year survival that we estimated for sakers predicts few

Table 2. Turnover of adult saker falcons in northern Kazakhstan in 1993–1994, as deduced from DNA profiles of nestlings. No parents changed if between-year band-sharing coefficients (BSCs) did not differ from within-year BSCs but did differ from that of unrelated birds. One parent changed if between-year BSCs differed from within-year BSCs and from the BSC of unrelated birds. Both parents changed if between-year BSCs differed from within-year BSCs but not from the BSCs of unrelated birds.[a]

| | Sample | | | Band–sharing coefficients | | | | | | | | |
| | | | Within yr | | | Between yr | | | Parents changed | Between vs. within yr | Between yr vs. unrelated |
Site	Yr	Interval(s)	n	$\bar{x}$	Range	n	$\bar{x}$	Range			
2	1994, 1996	2	4	0.74	0.69–0.78	6	0.74	0.69–0.86	0	ns	***
4	1994, 1995	1	9	0.72	0.55–0.86	5	0.67	0.61–0.71	0	ns	***
6	1993, 1994	1	3	0.75	0.60–0.80	3	0.80	0.69–0.84	0	ns	**
10	1993, 1996	3	6	0.68	0.60–0.76	4	0.58	0.46–0.67	0	ns	***
11	1993, 1994	1	6	0.57	0.41–0.72	9	0.55	0.35–0.68	0	ns	**
12	1994, 1995	1	3	0.53	0.47–0.58	3	0.52	0.46–0.59	0	ns	***
15	1994, 1997	3	9	0.56	0.40–0.68	5	0.52	0.45–0.64	0	ns	***
16	1994, 1995	1	12	0.68	0.56–0.82	16	0.59	0.50–0.72	0	ns	***
21	1995, 1996	1	15	0.73	0.61–0.86	20	0.75	0.64–0.88	0	ns	***
21	1996, 1997	1	12	0.73	0.61–0.86	16	0.76	0.67–0.88	0	ns	***
2	1996, 1997	1	6	0.75	0.69–0.81	4	0.52	0.38–0.64	1	*	*
3	1994, 1995	1	10	0.69	0.50–0.93	10	0.29	0.19–0.45	1	***	**
5	1994, 1996	2	3	0.76	0.70–0.83	3	0.50	0.40–0.59	1	*	*
17	1994, 1996	2	4	0.60	0.50–0.68	6	0.33	0.25–0.48	1	**	*
1	1994, 1997	3	7	0.61	0.51–0.90	8	0.19	0.10–0.33	2	***	ns
6	1994, 1997	3	9	0.75	0.60–0.84	12	0.21	0.17–0.26	2	***	ns
13	1995, 1996	1	3	0.58	0.42–0.86	3	0.10	0.04–0.16	2	*	ns
Total	28					10					

[a] Mann–Whitney U tests, 1–tailed: ns = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

adults relative to the young they produced. Nevertheless, a saker population with the survival and productivity estimates of the northern population would remain stable with an average of only 63% of falcons beyond their first year producing clutches. We let $\omega = 18$ years, in the absence of data on maximum breeding age of sakers, but the adult breeding rate changes only to 62% with $\omega = 20$ years. We had too few data to separately calculate the survival of juvenile males and females.

The models predicted yields of juveniles or adults that could be removed sustainably if adult breeding rates were increased to 85% and 100% (Table 4). We compared sensitivity across species by reducing adult and juvenile survival rates by 5% from estimated values (SE = 5% for sakers, 4–6% for buzzards, 6–9% for goshawks). The predicted yield of nestling buzzards and female goshawks exceeded 50% at the 85% breeding rate and remained ≥40% even with reduced adult survival. However, the

yields that the models predicted for sakers and male goshawks did not exceed 20%, even with full breeding of adults, with the 5% survival reductions. In order to compare yields across age categories, we expressed numbers of adults for harvest as a percentage of the juvenile cohort. The estimated sustainable harvest for adults was never appreciably more than half that for juveniles, and it was least for sakers.

The known removal of nestlings from southern nests reduced the productivity to 0.71 young per clutch (15 young in 21 breeding attempts) during 1994–1996 (Table 3). Other nests that failed may also have been robbed, reducing productivity. At a productivity of 0.71 young per clutch, a model that utilized the adults and young of 1993 and the productivity of 1994–1996 predicted an annual decline of 12% with 100% of adults breeding, which was less than the observed annual decline of 40%. However, many adult falcons were trapped in the southern study areas where they

Table 3. Breeding data for saker falcons during 1993–1996 at 2 study areas in Kazakhstan.

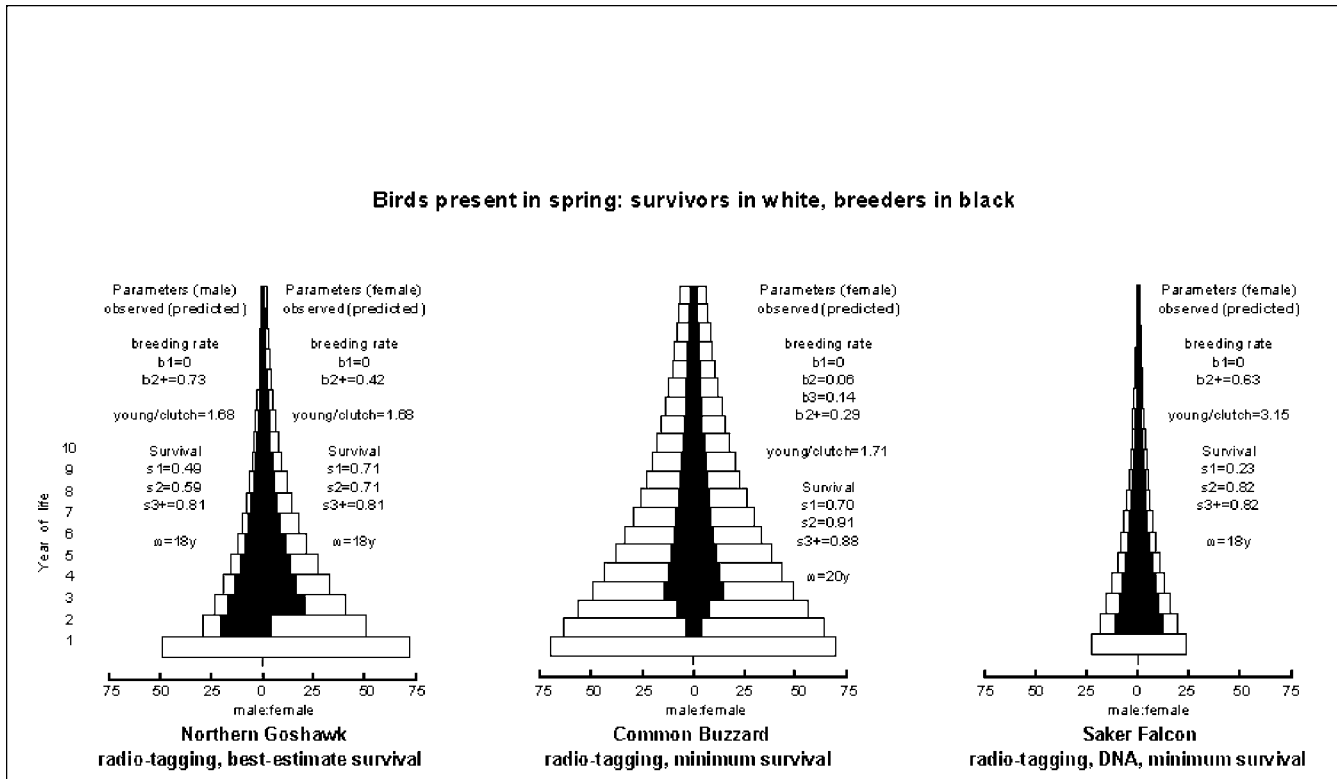| Study area | Yr | No. of nests | | | | Fledged young/ | |
		Checked	Occupied	Robbed	Successful	Successful nest	Occupied nest
Northern	1993	18	16	1	15	4.1	3.8
	1994	18	16	0	12	3.2	2.4
	1995	18	17	0	15	3.7	3.3
	1996	18	14	2	12	3.5	3.0
Southern	1993	21	14	7	6	4.2	1.8
	1994	22	10	5	4	2.0	0.8
	1995	22	8	6	2	3.5	0.9
	1996	21	3	3	0	0	0.0

Figure 1. Age-specific survival and breeding diagrams for populations of Swedish goshawks, British buzzards, and Kazakhstani saker falcons, showing the percentage remaining alive (open bars) and breeding (in black) in spring of each year of life for each species; $s1$, $s2$, and $s3+$ are the survival rates in years 1, 2, and older; $b1–b3+$ are observed or estimated proportions breeding; y young are produced per clutch; ω is maximum age (yr).

remained resident and therefore vulnerable during the autumn trapping season, unlike the population in the north, which was subject to trapping only during migration. The extent of trapping adults near southern breeding cliffs was anecdotally large but could not be measured. Removing 55% of the adults annually would have produced the observed decline in the southern population.

DISCUSSION

These results show the progression of techniques that now allow rapid sustainability modeling for harvested populations of wildlife. With data from only 4 years of field study,

we were able to estimate sustainable levels of take for a population of a heavily utilized species, the saker falcon. Despite the estimation by radiotagging of a much lower juvenile survival for sakers (23%) than in preceding studies of goshawks and buzzards (49–71%), the high productivity of sakers still permits an appreciable residual yield, estimated as up to 37% for the juvenile cohort. In contrast, maximum yield for harvesting adults was 1/7 as many birds (10% of their population), and a rapid population decline in one area could be explained by substantial over-harvest of adults.

Yield estimates from ASSAB models will be too high if birth or survival rates are overestimated. Productivity of

Table 4. Sustainable yields of Swedish goshawks, British buzzards, and Kazakhstani saker falcons, estimated from population models by increasing breeding rates to 85% and 100%. We ran models at observed survival rates and with 5% reductions in juvenile or adult rates (to mimic harvest).

	% breeding for adult							
	M goshawks		F goshawks		Common buzzards		Saker falcons	
Conditions for yield estimation	85	100	85	100	85	100	85	100
With observed survival								
Juv yield (as % of fledged juv cohort)	16	28	53	60	66	71	26	37
Annual ad yield (as % of total ad population)	3	6	16	21	15	17	6	10
Ad yield (as % of fledged juv cohort)[a]	3	7	26	28	35	35	4	5
With survival reduced by 5%								
Survival reduced for juv: juv yield (%)	6	20	49	57	63	68	5	19
Survival reduced for ad: juv yield (%)	0	7	40	49	50	58	2	16

[a] Numbers harvestable as adults are appreciably larger than percentages where there are many nonbreeding adults (e.g., among buzzards and female goshawks).

sakers in the northern area used for modeling was unlikely to have been biased upward by failure to record breeding failures at unknown nests because sakers and the eagles whose nests they used had been studied there for >25 years (Bragin 1986, Bragin and Katzner 2004). The adult survival rate from DNA-fingerprinting would have been biased upward if death caused >1 partner change in 4 intervals of >1 year between blood samples (Table 2), but it would have been biased downward if sakers changed partners or nest sites without dying. The adult survival estimate of 82% was below the 83–88% estimates for goshawks and buzzards and relatively low among estimates from banding of 80–90% for other large falcons (Enderson 1969, Mearns and Newton 1984, Cade et al. 1988). Banding will give relatively accurate estimates of adult survival if age-specific recovery bias varies less among adult age categories than between adults and juveniles (Catchpole et al. 1995), and banding did give the same estimates as radiotagging for goshawks and buzzards (Kenward et al. 1999).

The 23% survival estimate for first year sakers was remarkably low compared with the estimates of 58% for goshawks and 66% for buzzards. Four possible reasons for underestimation include 1) radio failures, 2) adverse impact of radios, 3) poor philopatry, and 4) under-recording of birds that returned to natal areas. As well as the low (7%) radio-failure rate on buzzards, comparison with other markers on buzzards and red kites (*Milvus milvus*) indicated no adverse impacts on survival from the same tag design (Kenward et al. 2000, Dixon 2001). Prairie falcons (*Falco mexicanus*) with a similar harness design reared broods as successfully as those without tags (Vekasy et al. 1996). The similar recapture rates of sakers with and without tags in autumn suggest similar survival rates to that point, although samples are too small to be sure that adverse effects were absent. Furthermore, although poor philopatry cannot be ruled out, similar monitoring techniques detected natal visits in spring by all prebreeding buzzards that emigrated >50 km (Walls and Kenward 1998), so detection of philopatric survivors may have been adequate.

All 4 sources of survival underestimation could be checked by further work to record bands or transponders on breeding recruits (1,4), by comparison of return rates for birds with small tail-mount radios (2), and by tracking from satellites (Fuller et al. 1998) to record philopatry (3). These sources of bias would make the saker yield estimates (Table 4) conservative, as would any breeding by first-year birds (Craig et al. 2004). However, such breeding was recorded only in the southern study area and not in the modeled northern population. With higher breeding rates of 35% recorded for first-year goshawks (Nielsen and Drachmann 1999) and up to 40% for second-year buzzards (R. E. Kenward and S. S. Walls, Centre for Ecology & Hydrology, unpublished data), juvenile yields for buzzards and goshawks would be about 5% above those predicted (Table 4).

The low rate of return to natal areas could also reflect trapping on migration. The 8 band returns from the 126 northern falcons underestimate the true harvest because only one band was reported from 4 falcons in which microtransponders were recorded. As an illustration only, a band reporting rate of 1 in 4 (25%) would estimate a harvest of 32 birds (25%) from the 126 marked. The equivalent figure for the south would be 20 of 45 young (44%). With widespread marking to increase sample sizes, correction for band removal by detection of microtransponders could be used to refine estimation of harvest rates and (through mark–recapture methods) of population sizes.

There were too few data to separate survival of male and female sakers, but because falconers prefer the larger females (Allen 1982), this separation would be highly desirable. Moreover, the greater first year survival of female goshawks (71%) than of males (49%) reflected mean mass of 1,250 g and 850 g, respectively (Marcström and Kenward 1981). Female and male sakers are less dimorphic than goshawks, weighing 1,080 g and 820 g, respectively. However, high female-biased returns, despite preferential trapping of females, and a tendency for female birds to be less philopatric than males (Greenwood 1980, Newton 1998) may indicate that female sakers survived better than males, perhaps because they are better than males at carrying radiotags on a lengthy migration.

In 26 early analyses of raptor band recoveries, the highest estimate of first-year survival was 50%, with <40% in 17 cases (Newton 1979). The 58% and 66% estimates from radiotracked goshawks and buzzards in our models (Table 4) were therefore comparatively high, but they correctly predicted breeding rates of goshawks and buzzards from observed productivity. At balance, the goshawk model with observed survival and breeding rates predicted that 73% of adult males and 42% of females would produce clutches; clutches were produced by 71% of 28 adult males and 36% of 42 females that were radiotagged in winter foraging areas (Kenward et al. 1999). Similarly, buzzard models predicted that only 21% of birds present in spring (including juv) would produce clutches, or 25% if 10% of juveniles emigrated; mark-resighting and corrected-transect estimates of buzzard numbers in areas with nest counts indicated that 21–25% produced clutches (Kenward et al. 2000).

High survival of juveniles predicts large proportions of nonbreeding adults in stable raptor populations (Hunt 1998). Despite a first-year survival as low as 23%, a breeding rate of only 63% for adult sakers balanced the ASSAB model. This was lower than the 73% predicted (and 71% observed) for male goshawks, so yields estimated for sakers were higher than for male goshawks, which could not sustain any yield with reduced adult survival and only 85% breeding (Table 4). However, the low survival estimate for juvenile sakers produced a model that was more sensitive than for other species to a further reduction in survival of juveniles. Moreover, sustainability of the modeled saker population depends on the relatively high production of 3.14 young per clutch compared with 1.68–1.71 young per clutch for goshawks and buzzards, so the number of adults that could be removed relative to juveniles was least for sakers.

MANAGEMENT IMPLICATIONS

The models in this report give conservative yields if raptors are harvested as nestlings because 1) they lack possible compensation in survival or productivity at reduced non-breeder density (Haukioja and Haukioja 1970, Newton 1979) and 2) birds were already being removed from all 3 populations by shooting and trapping. The estimates are, in effect, minimum sustainable yields. Such models to estimate conservative yields can now be built rapidly if nestlings are fitted with reliable and safe radiotags and adult turnover is estimated from DNA analyses or other techniques. For a species capable of producing 3–5 young, like sakers, a preliminary model could be completed in 2 breeding seasons, with blood from young in 15–20 nests (representing 30–40 adults) in each year and radiotags on 30–40 young in the first year. Pilot work to verify by markers that the parentage is as predicted by band-sharing coefficients would be desirable. Alternatively, with recent improvements in techniques for extracting DNA (Taberlet and Luikart 1999, Rudnick et al. 2005), collection of molted feathers from parents could be used to estimate adult turnover (and recruitment of DNA-profiled young) without need either of trapping adults or of large broods.

Limits of 5% for permissible yield have been based on banding data in similar models of other raptor species used for falconry in North America (Millsap and Allen, 2006). Conservative limits have merit for social sustainability of harvest, and where juvenile survival is as low as may be the case for sakers, any harvest of adults seems undesirable. Generally low limits can also motivate research either to justify social acceptability of higher limits for particular species or for particular sexes of dimorphic species, or where harvests may have environmental economic benefits such as mitigating predation problems or conserving habitats.

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