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# IS FLEDGING SUCCESS A RELIABLE INDEX OF FITNESS IN NORTHERN GOSHAWKS?

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ABSTRACT.—Fledging success is often assumed to be a reliable index of reproductive success (i.e., fitness) in the ornithological literature. We examined the validity of this assumption in a large population of Northern Goshawks (*Accipiter gentilis*) on the Kaibab Plateau, Arizona, at both the population and individual levels. We used mark-recapture data from 558 fledglings produced at 494 nests over a 10-yr period to assess the hypothesis that the number of fledglings returning to breed from an annual fledgling cohort is positively correlated with the size of the cohort. Natal philopatry was low and recruitment was gradual: only 48 fledglings (8.6%) returned to breed between 2–8 yr of age ($\bar{x}$ = 3.5 yr). We found no evidence that the breeding population produced more local recruits in years of high fledgling production than in years of low fledgling production. At the individual level, however, fledgling production for 290 breeding adults was related to their contributions to the future breeding population. Variation in fitness potential among territorial adults was high, as only 20% of the breeding population produced nearly 50% of the fledglings and 84% of the local recruits during the study. Our results indicate that measures of annual productivity for a large breeding population were not reflective of reproductive success, whereas measures of individual productivity were. We conclude that fledging success of individual goshawks is a reliable index of fitness, but that population productivity is a poor predictor of local recruitment.

KEY WORDS: *Northern Goshawk;* Accipiter gentilis; *fitness; individual heterogeneity; Kaibab Plateau; recruitment; reproductive success.*

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¿CONSTITUYE EL ÉXITO DE EMPLUMAMIENTO UN ÍNDICE CONFIABLE DE ADECUACIÓN BIOLÓGICA EN *ACCIPITER GENTILIS*?

RESUMEN.—En la literatura ornitológica, a menudo se asume que el éxito de emplumamiento representa un índice confiable del éxito reproductivo (i.e., adecuación biológica). Examinamos la validez de este supuesto en una población de gran tamaño de *Accipiter gentilis* en Kaibab Plateau, Arizona, tanto a nivel de población como de individuo. Usamos datos de marcado y recaptura de 558 volantones provenientes de 494 nidos a lo largo de un período de 10 años para evaluar la hipótesis de que el número de volantones que regresan a reproducirse de una cohorte anual de volantones está positivamente correlacionado con el tamaño de la cohorte. La filopatría natal fue baja y el reclutamiento fue gradual: sólo 48 volantones (8.6%) regresaron a reproducirse con entre dos y ocho años de edad ($\bar{x}$ = 3.5 años). No encontramos evidencia de que la población reproductiva produjo más reclutamientos locales en años de alta producción de volantones que en años de baja producción. A nivel individual, sin embargo, la producción de volantones correspondiente a 290 adultos reproductivos se relacionó con sus contribuciones a la futura población reproductiva. La variación en la adecuación biológica entre los territorios de los adultos fue alta, ya que sólo el 20% de la población reproductiva produjo cerca del 50% de los volantones y el 84% de los reclutamientos locales durante el estudio. Nuestros resultados indican que las medidas de productividad anual de una población reproductiva de gran tamaño no reflejaron el éxito reproductivo, mientras que las medidas de productividad individual si lo hacen. Concluimos que el éxito de emplumamiento individual de *A. gentilis* representa un índice confiable de adecuación biológica, pero que la productividad a nivel poblacional predice de modo inadecuado el reclutamiento local.

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In birds, a commonly measured reproductive variable used to assess population performance over time is fledging success (the number of young that fledge per nest). A widely held assumption in avian studies is that fledging success is a reliable index of reproductive success (the number of offspring that survive to become breeding adults) and thus, fitness (Endler 1986, Weatherhead and Dufour 2000, Keedwell 2003). However, the spatial and temporal scales over which many populations are studied may not correspond well with the spatial extent of natal dispersal or the time periods over which recruitment occurs. These limitations, superimposed on a variety of stochastic factors, could easily disrupt the relationship between fledging success and fitness. Nevertheless, researchers often assume this relationship is positive, in part, due to the difficulties associated with estimating pre-breeding survival and emigration rates, even in long-term banding studies. Difficulties in attaining direct measures of reproductive success are therefore exemplified in long-lived, wide-ranging species that occur at low densities, have low natal philopatry, elude detection when not breeding, and initiate breeding at a delayed age (Weatherhead and Dufour 2000).

The Northern Goshawk (*Accipiter gentilis*) is a long-lived raptor that occupies mature temperate and boreal forests throughout the Holarctic (Squires and Reynolds 1997). The goshawk is a socially monogamous, territorial species that lays one clutch per year (Reynolds et al. 1994, Kennedy and Ward 2003). Although several studies have documented extensive temporal variation in fledging success in goshawk populations (e.g., McClaren et al. 2002, Reynolds and Joy in press), none have addressed the relationship between fledging success and local recruitment. The strength of this relationship is particularly relevant when the dynamics of a local population are more heavily reliant on external recruitment (i.e., immigration) than internal productivity, which may occur when natal philopatry is low and adult site fidelity is high (Stacey and Taper 1992, Martin et al. 2000). While mate and site fidelity in adult goshawks is high (75–95%; Detrich and Woodbridge 1994, Reynolds and Joy in press), the degree of natal philopatry is largely unknown due to low juvenile recapture probabilities, few recoveries of banded nestlings, and a general lack of information on the extent of natal dispersal (Kennedy and Ward 2003, but see Wiens 2004). However, molecular evidence has shown that gene flow among subpopulations of goshawks over large geographic areas is high (Sonsthagen 2004, Bayard de Volo et al. 2005), indicating that juveniles may disperse over long distances because adults rarely disperse once they have settled on a breeding territory. Juvenile survival is one of the most difficult demographic parameters to estimate precisely in goshawks (Kennedy 1997, Wiens 2004), further emphasizing the need to assess the assumed relationship between fledging production and reproductive success.

In this paper we evaluate whether fledgling success is a reliable predictor of reproductive success in goshawks. We examined this relationship at both the population and individual levels using a 13-yr mark-recapture (resight) data set obtained from a breeding population of goshawks exceeding 120 pairs on the Kaibab Plateau, Arizona. Our investigation was inspired by studies showing a positive relationship between fledging success and recruitment in bird species such as Red-winged Blackbirds (*Agelaius phoeniceus*), Eurasian Sparrowhawks (*Accipiter nisus*), Ural Owls (*Strix uralensis*), and Osprey (*Pandion haliaetus*; Weatherhead and Dufour 2000, Newton 1989a, Saurola 1989, Postupalsky 1989, respectively). At the population level, we assessed the hypothesis that the number of fledglings produced annually is positively correlated with the number of individuals from annual cohorts that were eventually recruited into the local breeding population. At the individual level, we anticipated that total fledgling production of color-marked male and female adult (≥2 yr old) goshawks would be positively related to the number of their descendants that were recruited into the local breeding population. In examining our hypotheses, we also report on local recruitment and ages at first breeding for goshawks on the Kaibab Plateau.

## METHODS

**Study Area and Field Procedures.** The study area included all the coniferous forest above 2182 m elevation on the Kaibab Plateau of northern Arizona. This 1732 km$^2$ area included the northern portion of the Kaibab National Forest and the Grand Canyon National Park (North Rim). The Kaibab Plateau is a large (95 × 55 km), oval-shaped plateau that rises from a shrub-steppe plain at 1750 m elevation to the highest point at 2800 m and is dissected by moderately sloping valleys (Rasmussen 1941). Forests of the Kaibab Plateau are isolated from similar forests by variable distances (35–250 km) of pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodland, and sagebrush (*Artemisia* spp.) plains. See Reynolds et al. (1994) and Reynolds et al. (2005) for further detail on the study area, its management history, and protocols used to locate, survey, and monitor goshawk breeding areas.

We defined a territory as a breeding area used, but not necessarily defended against conspecifics, by a single pair of goshawks during a breeding season (Reynolds et al. 2005). During 1991–2003, a high density of regularly-spaced goshawk breeding territories were identified on the Kaibab Plateau (Reich et al. 2004, Reynolds et al. 2005). Territories contained multiple alternate nests that were used one or more times over the years by goshawks. We visited all nests in early spring of each year to estimate occupancy and reproductive status of territorial pairs. If goshawks were not using a known nest, a three-stage territory survey protocol (Reynolds et al. 2005) was used to determine territory status. We classified a territory as "*active*" when eggs were laid, "*occupied*" when adult goshawks were observed on two or more occasions in the vicinity of a nest (or a single observation of an adult in combination with observations of molted feathers, feces, and fresh nest construction), and "*unknown*" if eggs were not laid and no evidence of goshawk occupancy was found (Reynolds et al. 2005). We determined nest fate (successful = fledged ≥1 young; failed = eggs laid but no fledglings produced), nest productivity (number of fledglings), and identity of adults during weekly visits to *active* territories. For our purposes here, we defined the number of young fledged as the number of nestlings present at the time of banding (ca. 1 wk prior to fledging). Nesting adults were captured, measured, sexed, and aged during the mid–late nestling period following methods described in Reynolds et al. (1994); nestlings were captured by climbing nest trees during the last week of the nestling period (mid–late June). Sex of nestlings was assigned on the basis of body mass, tarsometatarsal length, and toepad-length measurements (Wiens 2004). All captured hawks received a U.S. Geological Survey aluminum leg band and an anodized colored leg band with a unique alpha-numeric code (Arcraft Sign and Plate Co., Edmonton, Canada) readable to 80 m with 40–60× spotting scopes.

**Age at First Breeding and Local Recruitment.** We considered a goshawk to have been recruited locally if it was banded as a nestling on the study area and later observed breeding in the study population. Thus, hawks classified as "local recruits" had to have been recaptured or resighted at an active territory on the Kaibab Plateau. To attain an unbiased estimate of the age at first breeding, we included only banded (known-aged) hawks that we were confident had been detected on their first breeding attempt. This meant that banded recruits had to have been resighted on territories where the same-sex occupant during the prior year was known. Estimated ages at first breeding could have been biased high by breeding dispersal (i.e., undetected movement among territories between successive breeding attempts). However, this bias was likely to be small because <6% of adult goshawks moved to a different territory between successive breeding attempts (R. Reynolds unpubl. data). To attain a mean estimate of local recruitment, we subtracted the number of nestlings that were too young (based on the median age at first breeding) to have attained breeding territories by spring 2003 from the total number of nestlings banded during 1991–2003. Hence, local recruitment was calculated as the total number of banded recruits detected during 1991–2003 divided by the total number of nestlings banded during 1991–2000.

**Population Productivity.** We were unable to capture and mark all nestlings produced in some years because several nests were not located until after fledging or, rarely, a nest tree was unsafe to climb. Thus, the number of young banded represented a portion (69% during 1991–2003) of the known number of young that actually fledged. For this reason, we defined "productivity" as the number of young banded. We assumed that banded young comprised a representative sample in terms of population productivity and local recruitment. Using the number of young banded annually, we assessed whether the size of each annual fledgling cohort was correlated with the number of local recruits originating from each cohort. We conducted analyses with sexes combined and then separately for males and females. Data were examined by sex for two reasons. First, patterns of post-fledging mortality have been found to differ for male and female goshawks on the Kaibab Plateau (Wiens 2004). Second, natal dispersal distances may differ between sexes (Greenwood and Harvey 1982, Byholm et al. 2003). One or both of these factors could result in sex-dependent local recruitment. For sex-specific analyses, the number of individuals of each sex that successfully recruited from a fledgling cohort was assessed relative to the total number of individuals of each sex that were banded as nestlings.

**Individual Productivity.** To examine the relationship between total fledgling production of individual adult goshawks and recruitment success of their offspring, we calculated the number of banded fledglings produced by each color-marked adult that bred during 1991–2000. As in the population-level analysis, excluding fledgling productivity during 2001–03 ensured that all fledglings in our analysis had at least three years to acquire a breeding territory and be detected. We then related the number of banded fledglings produced by each adult to the total number of their offspring that had successfully recruited to the local breeding population by 2003. We used fledgling production by adults during the study period rather than lifetime productivity because our interest was in the reliability of individual fledging success as a measure of an individual's fitness potential, regardless of how often they bred or how long they had occupied a breeding territory. Nonetheless, lifetime fledgling production was captured for nearly all goshawks included in our analysis because of the duration of our study relative to the number of years goshawks successfully laid eggs ($\bar{x}$ = 2.1 yr, min. = 1 yr, max. = 10 yr, 1991–2004; R. Reynolds unpubl. data). We assumed that adults captured or resighted at a nest were indeed the biological parents of the nestlings banded at that nest. In raptors, females are often alone before and during egg laying while their mates forage, which could result in extra-pair fertilizations by conspecific males (Reynolds and Linkhart 1990, Negro et al. 1996, Gavin et al. 1998). Although extra-pair fertilizations could confound the relationship between fledgling success and recruitment, genetic evidence demonstrated that extra-pair fertilizations are infrequent for goshawks on the Kaibab Plateau (Gavin et al. 1998).

**Data Analysis.** At the population level, we used Spear-

Table 1. Northern Goshawk survey effort, banding activity, and local recruitment (banded nestlings from annual cohorts that eventually returned to breed) on the Kaibab Plateau, Arizona, 1991–2003.

| YEAR | TERRITORIES SURVEYED | USED NESTS (%)[a] | ADULTS BANDED | NESTLINGS BANDED | NESTLINGS RETURNED |
|---|---|---|---|---|---|
| 1991 | 37 | 36 (97) | 48 | 46 | 8 |
| 1992 | 64 | 59 (92) | 43 | 32 | 2 |
| 1993 | 82 | 67 (82) | 30 | 62 | 4 |
| 1994 | 88 | 21 (24) | 13 | 18 | 2 |
| 1995 | 99 | 53 (54) | 39 | 52 | 7 |
| 1996 | 105 | 46 (44) | 18 | 41 | 1 |
| 1997 | 106 | 31 (29) | 15 | 36 | 9 |
| 1998 | 109 | 58 (53) | 37 | 84 | 9 |
| 1999 | 113 | 57 (50) | 14 | 76 | 5 |
| 2000 | 120 | 66 (55) | 33 | 111 | 1 |
| 2001 | 120 | 30 (25) | 5 | 31 | 0 |
| 2002 | 121 | 21 (17) | 5 | 16 | 0 |
| 2003 | 121 | 10 (8) | 2 | 9 | — |

[a] Percent of total territories under study that contained used nests (eggs laid).

man correlation coefficients ($r_S$) to characterize the strength of the relationship between the size of each annual fledgling cohort and the number of local recruits originating from each cohort. We estimated the expected number of fledglings recruited from each annual cohort by multiplying our overall estimate of local recruitment by cohort size. A chi-square analysis was then used to evaluate possible deviations from the expected number of fledglings recruited from each cohort. At the individual level, we used generalized linear models (PROC GENMOD; SAS Institute 1999) to investigate our prediction that total fledging production by individual adults would be positively related to the number of local recruits each produced. Specifically, we used Poisson regression in a log-linear model in which a count of recruits produced per adult was the response variable and the number of banded fledglings produced per adult was assessed as an explanatory variable. Chi-square tests or a Fisher's exact test were used to examine potential sex-related differences in the age at first breeding and local recruitment. All analyses were conducted using SAS (ver. 8.2). Results are reported as means ± SE, with 95% confidence intervals (CI).

## RESULTS

The number of territories surveyed increased from 37 in 1991 to 121 in 2003 (Table 1). All but two of the 121 territories contained nests with eggs or young in one or more years of the study. The exceptions were territories where goshawks occupied newly built or reconstructed old nests, but did not lay eggs. The percentage of territories under study that contained nests with eggs or young varied substantially among years, ranging from 8% in 2003 to 97% in 1991 (Table 1). This resulted in highly variable fledgling production among years, ranging from only 9 fledglings in 2003 to 111 in 2000. Of the 13-yr total of 555 nests with eggs, 447 (80.5%) adult pairs fledged 897 young successfully (614 of which were banded), and 108 (19.5%) pairs lost their clutch during the incubation or nestling stages.

**Age at First Breeding and Local Recruitment.** In the 10 yr that we included for fledgling production (1991–2000), we banded 558 nestlings (278 females and 280 males) at 494 nests (Table 1). Forty-eight (8.6%) of these nestlings returned to breed on the study area–26 (9.4%) females and 22 (7.9%) males. Nestling return rates were similar between the sexes ($\chi^2 = 0.40$, df = 1, $P = 0.53$). Ages at first breeding could be determined with confidence for 28 of 48 fledglings that returned to breed (17 of 26 females and 11 of 22 males; Fig. 1). These hawks initiated breeding between 2–8 yr of age (3.5 ± 0.32 yr, 95% CI = 2.84–4.16, median = 3 yr). Only four hawks (all females) were older than 4 yr of age at first breeding. Differences between sexes in the age at first breeding were not supported (Fisher's Exact Test: $P = 0.49$). No hawks in first-year plumage were observed breeding at or occupying a nest during the 13-yr study. Two females banded as nestlings were later resighted in adult plumage occupying inactive breeding territories on the study area, and two locally banded nestlings were found breeding in forests beyond the Kaibab Plateau (Wiens 2004).

**Population Productivity.** We found no evidence

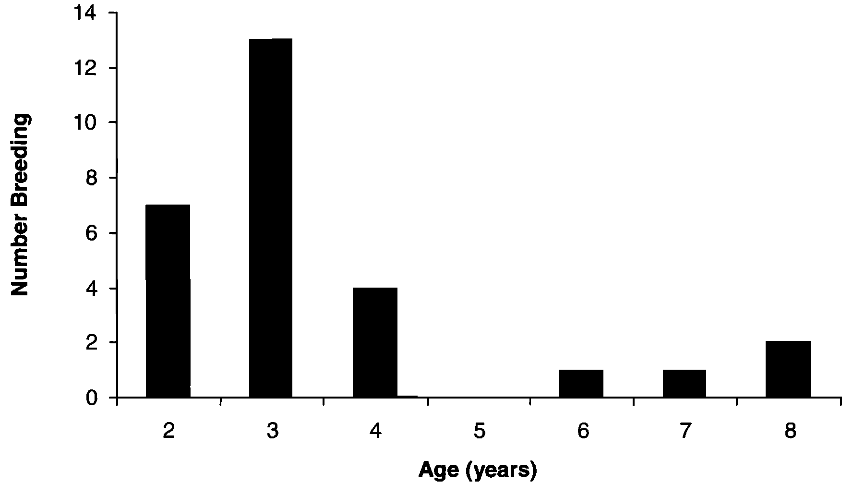


Figure 1. Distribution of ages at first breeding for 28 known-aged Northern Goshawks recaptured on their first breeding attempt on the Kaibab Plateau, Arizona, 1991–2003.

that the number of fledglings recruited from annual cohorts was correlated with cohort size ($r_s$ = 0.10, $P$ = 0.79, $N$ = 10; Fig. 2). Likewise, there was no evidence of a correlation between annual estimates of fledging production and recruitment when sexes were analyzed separately (females: $r_s$ = 0.24, $P$ = 0.50; males: $r_s$ = 0.11, $P$ = 0.76). The number of local recruits produced was significantly higher than expected for the 1991 (8 observed, 3.9 expected; $\chi^2$ = 4.13, df = 1, $P$ = 0.04) and 1997 (9 observed, 3.1 expected; $\chi^2$ = 11.25, df = 1, $P <$ 0.01) fledgling cohorts, but much lower than expected for the 2000 fledgling cohort (1 observed, 9.5 expected; $\chi^2$ = 7.65, df = 1, $P <$ 0.01). We found no other deviations in numbers of observed versus expected recruits in any other fledgling cohort. Thus, the 2000 fledgling cohort was the only one of the 10 cohorts in which significantly fewer fledglings returned to breed than expected. To ensure that including this year did not unduly bias

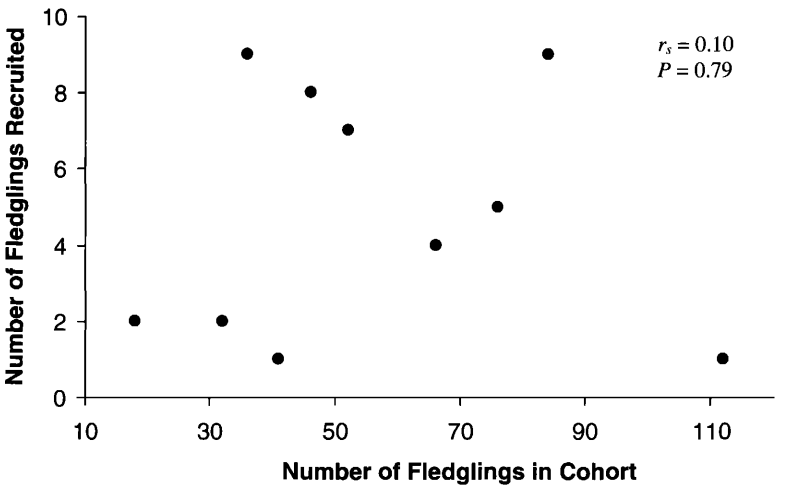


Figure 2. Number of locally produced Northern Goshawk fledglings recruited into the breeding population on the Kaibab Plateau, Arizona, relative to the number of young fledged within each annual cohort, 1991–2000. Each point represents one year.

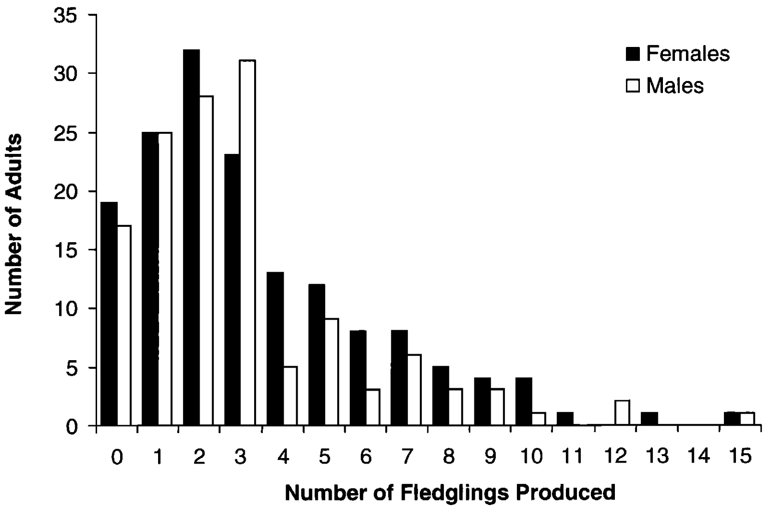


Figure 3. Fledgling production of 156 female and 134 male color-marked adult (≥2-yr-old) Northern Goshawks breeding between 1991 and 2000 on the Kaibab Plateau, Arizona.

our results, we reanalyzed the data without this cohort. Although this improved the relationship slightly, the size of a fledgling cohort was still a poor predictor of the total number of goshawks that returned to breed from the cohort (sexes combined: $r_s = 0.46$, $P = 0.21$, $N = 9$; females: $r_s = 0.52$, $P = 0.15$; males: $r_s = 0.46$, $P = 0.21$).

**Individual Productivity.** Fledging success was calculated for 156 females and 134 males breeding during 1991–2000 (Table 1). During this period, females spent between 1–7 yr as breeders (2.18 ± 0.11 yr; 95% CI = 1.96–2.40) and fledged between 0 and 15 young (3.39 ± 0.23 young; 95% CI = 2.93–3.85). Similarly, males also spent between 1 and 7 years as breeders (1.96 ± 0.11 yr; 95% CI = 1.73–2.18) and fledged between 0 and 15 young (2.98 ± 0.23 young; 95% CI = 2.51–3.44). The distribution of fledgling production among breeders was highly skewed, with most individuals producing few or no fledglings and only a few individuals having extremely high success (Fig. 3). In total, 156 adult females produced 529 fledglings and 134 adult males produced 399 fledglings (the remaining 29 and 159 banded nestlings were parented by unknown adult females and males, respectively). Thirty-six adults (19 females and 17 males) laid eggs but failed to produce fledglings.

The recruitment success of an adult's offspring was significantly related to the total number of fledglings the adult produced (sexes combined: regression slope coefficient, $\hat{\beta} = 0.22 \pm 0.03$, Wald $\chi^2 = 74.77$, df = 1, $P < 0.01$, $N = 290$; females: $\hat{\beta} = 0.22 \pm 0.04$, $\chi^2 = 38.2$, df = 1, $P < 0.01$, $N = 156$; males: $\hat{\beta} = 0.22 \pm 0.04$, $\chi^2 = 37.3$, df = 1, $P < 0.01$, $N = 134$; Fig. 4). We had two concerns regarding this result. First, we suspected that fledglings produced during the 2000 breeding season might not have had sufficient time to be recruited by 2003 (as was our concern in the population-level analysis). Second, there were 33 new unbanded adults (17 females and 16 males) who first bred in the study population in 2000 (Table 1). Several of these individuals also bred in subsequent years, so our initial analysis may have not represented their contributions adequately to fledgling production. To address these concerns, we reanalyzed the data without individual productivity and recruitment data from the 2000 breeding season. Excluding the 2000 breeding season had little effect on the strength of the relationship (sexes combined: $\hat{\beta} = 0.28 \pm 0.03$, $\chi^2 = 71.0$, df = 1, $P < 0.01$, $N = 257$; females: $\hat{\beta} = 0.28 \pm 0.05$, $\chi^2 = 37.1$, df = 1, $P < 0.01$, $N = 139$; males: $\hat{\beta} = 0.28 \pm 0.05$, $\chi^2 = 36.5$, df = 1, $P < 0.01$, $N = 118$). Thus, fledging success of individual goshawks could be taken as a reasonable index of their contributions to the future breeding population.

Both sexes exhibited similar patterns of variance in fledgling production and in the number of recruits they produced (Figs. 3, 4). Moreover, fledging success and contributions of offspring to the future breeding population varied extensively

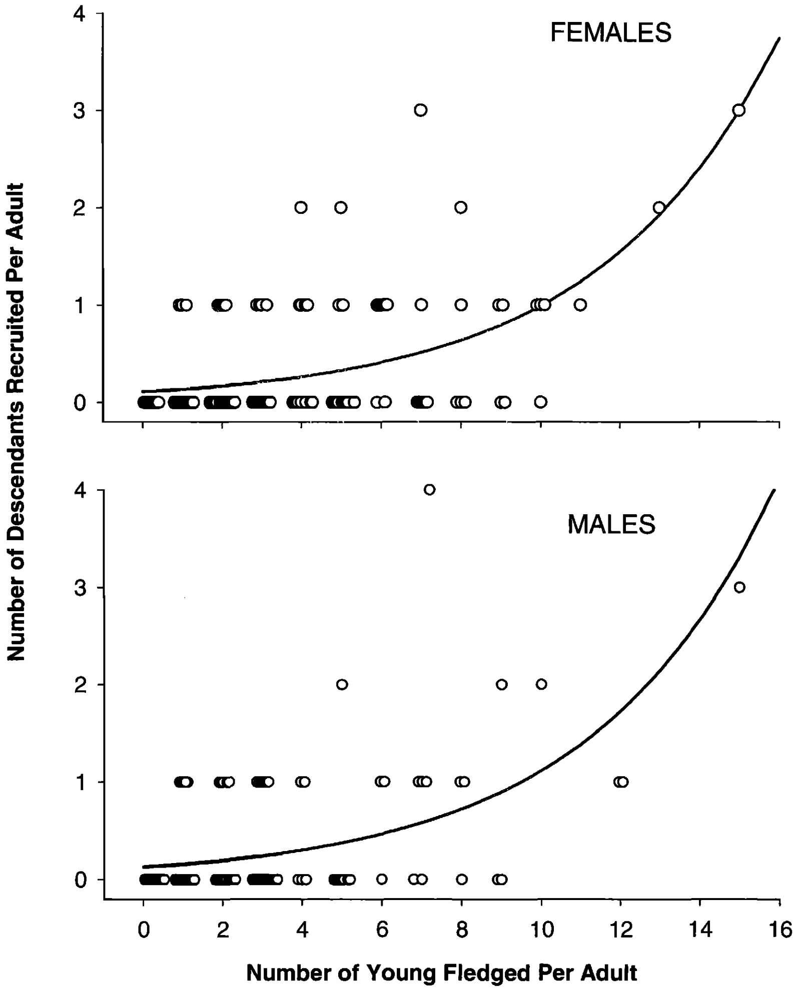


Figure 4. Number of descendants of individual female ($N = 156$) and male ($N = 134$) adult (≥2-yr-old) Northern Goshawks that successfully recruited into the breeding population in relation to the number of fledglings each adult produced between 1991 and 2000 on the Kaibab Plateau, Arizona. Each point represents an individual adult. Trend lines determined by Poisson regression with a log-link function (females: $\hat{y} = \exp[-2.217 + 0.221x]$; males: $\hat{y} = \exp[-2.056 + 0.217x]$).

among territorial hawks; 20% of adults breeding during 1991–2000 contributed nearly 50% of the fledglings and 83% of the local recruits produced during this time (Fig. 5). Of 290 breeding goshawks, 73 (25.2%) produced at least one local recruit each, seven (2.4%) produced two recruits each, and three (1%) produced three recruits each. One male produced four local recruits, but no female produced more than three. In tracking lineages up to three generations, three females left one breeding descendant each who also produced young that were recruited, and two males left one breeding descendant each who also produced young that were recruited.

## DISCUSSION

When measured at the population level, our results failed to support the hypothesis that fledging success is a reliable index of local recruitment in goshawks. When measured on an individual basis, however, adult fledging success was significantly related to local recruitment, indicating that total fledgling production by individuals was a more reliable index of reproductive success than a mea-

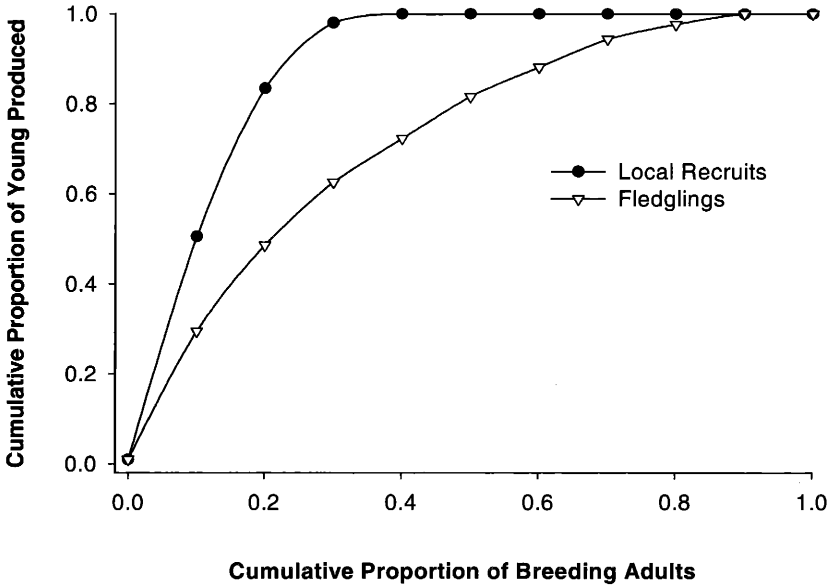


Figure 5. Individual variation in total fledgling production and reproductive success (number of offspring that were local recruits) among 290 color-marked adult (≥2-yr-old) Northern Goshawks breeding between 1991 and 2000 on the Kaibab Plateau, Arizona. Whereas 254 (88%) adults successfully fledged young, only 73 (25%) made contributions to the future local breeding population.

sure of annual productivity. Another important finding was that reproductive success varied widely among breeding adults. Thus, the relationship between fledging success and recruitment appeared to be highly dependent upon the disproportionate contributions of fledglings and recruits made by a relatively small number of adults rather than overall population productivity. Our results further demonstrate that recruitment of goshawks on the Kaibab Plateau was a gradual process (as shown by a wide range among individuals in the age at first breeding) and that local recruitment was relatively low (8.6%). Given that 25% of adults fail to return to reclaim their territory each year (Reynolds et al. 2004), external recruitment (i.e., immigration) would need to be ca. 16% to maintain a stable breeding population.

**Age at First Breeding and Local Recruitment.** Goshawks are capable of breeding in their first year of life, and the proportion of breeders in first-year plumage has been reported to be as high as 35–40% (McGowan 1975, Reynolds and Wight 1978, Speiser and Bosakowski 1991, Younk and Bechard 1994). The proportion of young hawks in a breeding population may be reflective of density-dependent processes driven by the availability of nesting territories, food, or mates (McGowan 1975, Newton 1989b, Ferrer et al. 2004). As breeder density and survival increases, fewer territories are available to prospective breeders, forcing socially subordinate younger hawks to wait, perhaps several years, to gain a breeding vacancy. Observations of individuals breeding in non-adult plumage may, therefore, reflect an important buffer mechanism compensating for an increased adult mortality rate (Ferrer et al. 2004). On the Kaibab Plateau, several demographic features such as a temporally stable adult survival rate (Reynolds et al. 2004), a high density of breeding territories (8.6/100 km$^2$; Reynolds et al. 2005), and strong adult fidelity to territory and mate (R. Reynolds unpubl. data) suggest that young goshawks prospecting for breeding opportunities are faced with the alternatives of delaying breeding altogether or dispersing to recruit elsewhere (Wiens 2004). That some individuals remain (or return) as floaters in the vicinity of their natal population on the Kaibab Plateau has been confirmed by radiotelemetry (Wiens 2004) and a quick replacement of territorial hawks following mortality (Reynolds and Joy in press). Collectively, these features could explain the relatively advanced age of first-time breeders as well as the low local recruitment level during our study. It is important to note, however, that these characteristics (territory density, adult fidelity, breeding age) appear to occur at higher levels on the Kaibab Plateau than reported for goshawks elsewhere.

**Population Productivity.** We found that the goshawk population on the Kaibab Plateau was no more successful in producing local recruits in years of high fledgling production than in years of low fledgling production. Thus, contrary to predictions, the size of an annual fledgling cohort was a poor predictor of local recruitment. In contrast, Weatherhead and Dufour (2000) found that local recruitment increased disproportionately with the size of Red-winged Blackbird fledgling cohorts, even though the overall return rate of banded nestlings in that study was small (2.4%) relative to our estimate for goshawks (8.6%). The strength of the relationship between population productivity and local recruitment, and our inability to detect such a relationship, may largely depend on the spatial extent of the study area relative to the extent of natal dispersal. For example, Red-winged Blackbirds disperse up to 40 km from natal territories (Moore and Dolbeer 1989), whereas young goshawks disperse up to 440 km from the Kaibab Plateau (Wiens 2004). The lack of a population-level relationship between fledging success and recruitment in our study may, therefore, simply reflect the difference between observing local recruitment within a relatively small subpopulation relative to general recruitment taking place over a regionally fragmented population that is connected by natal dispersal. Several lines of evidence indicate that most juveniles disperse long distances beyond the Kaibab Plateau in their first fall (Wiens 2004). Unfortunately, with the exception of two known cases of juvenile emigration, no information on the external recruitment success of locally-produced hawks exists for this study population.

Aside from a potentially inappropriate scale of investigation relative to the extent of the goshawk recruitment process, our data may have failed to support our hypothesis at the population level because of a lack of breeding opportunities during the later years of the study. During 2001–03, extreme drought conditions in northern AZ likely led to significant declines in goshawk prey populations (Salafsky 2004), and few adult pairs on the Kaibab Plateau attempted to breed. Under such poor breeding conditions, opportunities for inexperienced hawks attempting to breed for their first time were reduced. For the most part, adult goshawks could only be captured or resighted when breeding, so newly recruiting hawks that acquired a breeding territory but did not lay eggs may have gone undetected during 2001–03. Poor breeding conditions during the later years of our study could also explain the lower than expected recruitment success of fledglings produced in the 2000 breeding season. However, removing the 2000 cohort from the analysis failed to substantially improve the relationship between population productivity and local recruitment. Our chi-square analysis showed that fledglings produced in 1991 and 1997 were twice as likely to be recruited as expected. With the exception of the 2000 fledgling cohort, we found no other significant deviations in the number of local recruits expected. We suggest that high juvenile survival, density-dependent effects, or changes in resource availability may have contributed to the disproportionately high recruitment success of fledglings produced during 1991 and 1997.

**Individual Productivity.** If fitness is defined as the contribution of an individual's genotype to subsequent generations proportional to that of other individuals (Lincoln et al. 1998), then our results clearly show a difference in fitness among goshawks on the Kaibab Plateau. Our results indicated that the likelihood of an adult contributing offspring to the future breeding population on the Kaibab Plateau increased disproportionately with the number of fledglings it produced. Therefore, goshawks appear to be similar to other monogamous raptor species in that reproductive success varies widely among individuals (Newton 1989b, Hakkarainen et al. 1997, Marti 1997). As would be expected for a monogamous raptor in a population showing high fidelity to territory and mate and equal survival rates of males and females, the sexes showed similar patterns of variance in reproductive success. Indeed, a few territorial pairs exhibited disproportionately high fitness levels in terms of the number of years they bred, total fledgling production, and the number of their offspring that survived to become breeding adults. Factors not explored in this study, such as breeding age, habitat quality, individual quality (as determined by genetic forces), or climate may contribute to individual heterogeneity in goshawk reproductive success.

On the Kaibab Plateau, the mean reproductive lifespan of adults (first breeding to disappearance) is 2 yr, but a few adults were found to breed for as many as 10 yr (R. Reynolds unpubl. data). Adults who breed more often are likely to be more experienced, produce more fledglings, and show the highest fitness potential in terms of survival and reproduction (Cam et al. 1998). Newton and Rothery (2002), for example, demonstrated that almost all aspects of breeding performance in female Eurasian Sparrowhawks improved with age, but that the degree of improvement lessened with each successive year of life. In Denmark, Nielsen and Drachmann (2003) showed that fledgling production of European goshawks increased with female age from 1–7 yr, but declined thereafter. Similarly, Reynolds et al. (1994) reported a difference in fledging production between young-adult (second-year) and full-adult goshawks. These authors attributed changes in reproductive success to age-related trends in foraging efficiency, which could be buffered by pairing with more experienced mates.

Variation among individuals in fitness levels can have substantial effects on population growth, stability, and persistence (Bjørnstad and Hansen 1994, Conner and White 1999). Individual variation within raptor populations may be generated by temporal or spatial variations in resource availability and habitat quality (Hakkarainen et al. 1997, Franklin et al. 2000). Of particular interest is the relationship between individual fitness and habitat quality, as it is commonly supposed that birds prefer the habitat that will confer the greatest fitness (Fretwell and Lucas 1970). For goshawks, heterogeneity in fitness levels among territorial adults could be caused by spatial or temporal variations in food abundance, resource availability (as measured by qualitative differences in forest composition and structure among breeding areas), and individual hawk quality. However, recent efforts to detect spatial heterogeneity in goshawk reproductive parameters have had limited success. On the Kaibab Plateau, Joy (2002) ranked 101 goshawk territories as "high" or "low" quality based on differences in egg laying frequency and fledgling production. The length of time an adult female remained on a territory, breeder age, and the amount or spatial configuration of vegetative types within territories explained little of the variation (Joy 2002). Elsewhere, McClaren et al. (2002) found minimal spatial variation in the number of young fledged per nest among goshawk nest areas in three study sites in western North America. Given that these studies focused on territories (Joy 2002) and nest areas (McClaren et al. 2002) rather than individual goshawks, we suggest that undetected turnovers between territory or nest occupants of different age, experience, or genetic quality could mask existing spatial patterns in reproduction. For the purposes of identifying the determinants of habitat quality for goshawks, we believe our finding of individual variation in reproductive success highlights the need to partition the effects of individual hawk quality from habitat quality. By controlling for individual hawk quality, researchers can more precisely estimate the effects of habitat versus non-habitat factors on components of goshawk fitness. Given the hypothesized role of forest composition and structure in generating individual variation in goshawk reproductive performance, long-term demographic research based on color-marked individuals can provide a powerful tool to guide goshawk conservation and management.

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