

A SKEWED SEX RATIO IN NORTHERN GOSHAWKS: IS IT A SIGN OF A STRESSED POPULATION?

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ABSTRACT.—I examined 6 yr (1993–98) of data on Northern Goshawk (*Accipiter gentilis*) reproductive performance in east-central Arizona. Forty-four breeding territories were monitored over the 6-yr period, yielding 109 nesting attempts and 141 fledglings produced from 76 successful broods. Among the 63 broods from which sex of nestlings could be determined by measurements, 29% fledged one young, 54% fledged two young, and 17% fledged three young. The mean sex ratio across years was 1.93 ± 0.70 ($\pm 95\%$ CI) males/females (annual range 1.1:1–3:1). When combining all fledglings of known sex (76 males and 43 females), a 1.77:1 male to female sex ratio was significantly different from 1:1 ($P = 0.002$). A male-biased fledgling sex ratio may be explained by one or more of the following hypotheses: (1) more males were produced due to nutritional stress resulting in minimization of investment in the larger sex (females) and (2) fewer females were produced because of differential mortality due to exposure to the elements during the nestling stage. I propose that environmental stress in the form of exposure to the elements during a critical life stage (e.g., rainfall during the nestling stage), combined with limited food availability, may be driving the skewed sex ratios observed in this local Northern Goshawk population.

KEY WORDS: Northern Goshawk; *Accipiter gentilis*; nestling; sex ratio; sex allocation.

¿ES EL COCIENTE DE SEXOS SESGADO DE *ACCIPITER GENTILIS* UNA SEÑAL DE UNA POBLACIÓN ESTRESADA?

Resumen.—En este estudio examiné datos sobre el desempeño reproductivo de *Accipiter gentilis* recolectados a lo largo de seis años (1993–98) en el centro-este de Arizona. Un total de 44 territorios de nidificación fueron monitoreados a través de los seis años, observando un total de 109 intentos de nidificación y 141 volantones producidos en 76 nidadas exitosas. De las 63 nidadas en las que el sexo de los pichones pudo ser determinado mediante mediciones, el 29% produjeron un volatón, el 54% dos volantones y el 17% tres volantones. El cociente de sexos promedio a través de los años fue de 1.93 ± 0.70 ($\pm 95\%$ IC) machos/hembras (rango anual 1.1:1–3:1). Al combinar todos los volantones de sexo conocido (76 machos y 43 hembras), el cociente de machos a hembras resultante de 1.77:1 fue significativamente diferente de 1:1 ($P = 0.002$). Un cociente de sexos sesgado hacia los machos en los volantones podría explicarse por las siguientes hipótesis: (1) se produjeron más machos como consecuencia de estrés nutricional que llevó a minimizar la inversión en el sexo de mayor tamaño (hembras) y/o (2) se produjeron menos hembras como resultado de una mortalidad diferencial debida a la exposición al ambiente durante la permanencia de los pichones en el nido. Propongo que el estrés ambiental causado por la exposición a las condiciones ambientales durante una etapa crítica de la vida (e.g., la lluvia durante la etapa de crianza en el nido), combinado con la disponibilidad limitada de alimento, podrían estar determinando el sesgo en el cociente de sexos observado en esta población local de *A. gentilis*.

[Traducción del equipo editorial]

Female Northern Goshawks (*Accipiter gentilis*) are approximately 20–30% heavier than males (Newton 1979, Palmer 1988, Squires and Reynolds 1997). Larger offspring require more food to at-

tain fledging age, and thus are more susceptible to food shortages (Clutton-Brock et al. 1985, Teather and Weatherhead 1988, Anderson et al. 1993). An underlying assumption of an adjustable sex ratio is that parents should bias the sex ratio of their offspring toward the sex whose production will most increase their own fitness (Trivers and Willard

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1973, Clark 1978, Charnov 1982, Clutton-Brock 1986). The sex ratio at fledging should be the inverse of the ratio of the cost of producing each sex (Fisher 1930). Consequently, under times of limited prey resources the sex ratio should be biased toward the "cheaper sex" (in Northern Goshawks: the male; Howe 1977, Cronmiller and Thompson 1981, Teather and Weatherhead 1988). In sexually-dimorphic species, differential survival between the sexes is most likely due to differing nutritional requirements, with higher mortality incurred by the larger sex (Torres and Drummond 1997, Sheldon et al. 1998). However, this may be offset in Northern Goshawks by the tendency of the female nestlings to seize prey items more readily than males (Lee 1980).

Sex allocation in sexually dimorphic raptors has provided mixed observations. Studies have shown prevalence toward male fledglings in Golden Eagles (*Aquila chrysaetos*; Edwards et al. 1988), Harris's Hawks (*Parabuteo unicinctus*; Bednarz and Hayden 1991), Montagu's Harriers (*Circus pygargus*; Leroux and Bretagnolle 1996), and Cooper's Hawks (*Accipiter cooperii*; Rosenfield et al. 1996). Other studies showed prevalence toward female fledglings in Northern Harriers (*Circus cyaneus*; Balfour and Cadbury 1979), Bald Eagles (*Haliaeetus leucocephalus*; Bortolotti 1986), and Peregrine Falcons (*Falco peregrinus*; Olsen and Cockburn 1991). However, most studies on raptors have revealed equal sex ratios in offspring (Newton 1979). In some previous work on Northern Goshawks, the sex ratio for fledglings has been shown not to differ from 1:1 (Newton 1979, Reynolds and Joy 1998).

A male-biased fledgling sex ratio may be explained by one or more of the following hypotheses: (1) more males were fledged due to nutritional stress resulting in minimization of investment in the larger sex (females) during the nestling stage (Trivers and Willard 1973, Torres and Drummond 1997) and (2) fewer females were produced because of differential mortality due to exposure to the elements during the nestling stage with larger young exhibiting a higher mortality rate (Newton 1979:136–137). Hypothesis 1 above may be a direct product of adaptive selection, whereas hypothesis 2 may simply be a nonadaptive by-product of differential mortality. The purpose of this paper is to discuss these potential explanations for the sex ratio exhibited by Northern Goshawk fledglings in east-central Arizona.

STUDY AREA

The Sitgreaves portion of the Apache-Sitgreaves National Forest is located on the Mogollon Plateau in east-central Arizona and encompasses approximately 330 300 ha. Elevation ranges from 1768–2417 m. To the south, the study area is bounded by the Mogollon Rim, a large escarpment extending east across central Arizona and into New Mexico. To the east, the study area is bounded by the Springerville Ranger District boundary on the Apache National Forest. A wide range of vegetation communities occurs within the study area (Brown 1994). The Mogollon Rim edge is dominated by deep drainages with mixed-conifer communities of Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and ponderosa pine (*Pinus ponderosa*), with pockets of aspen (*Populus tremuloides*), New Mexico locust (*Robinia neomexicana*), and Gambel oak (*Quercus gambelii*). Ridgetops are generally dominated by ponderosa pine forest. To the north, as elevation decreases, a ponderosa pine/juniper-pinyon ecotone transitions to a juniper-pinyon woodland dominated by alligator juniper (*Juniperus deppeana*), Utah juniper (*J. osteosperma*), and Rocky Mountain pinyon pine (*P. edulis*). As elevation decreases further, a plains grassland community develops, dominated by blue grama (*Bouteloua gracilis*), sand dropseed (*Sporobolus cryptandrus*), and fourwing saltbush (*Atriplex canescens*).

METHODS

I monitored demographic parameters of a Northern Goshawk population on the Apache-Sitgreaves National Forest from 1993–98 and specifically noted the sex of fledgling birds. I visited occupied nests periodically during the breeding season (ca. late April–early August) to monitor status and productivity. An occupied nest was one in which at least one egg was laid (usually inferred by observing a bird in incubation posture). I estimated the ages of nestlings using a photographic guide produced by Boal (1994). Birds were deemed to have survived to fledge when they were greater than 80% of fledgling age (31 d old; Steenhof 1987). When nestlings were between 30–40 d old, I banded them with U.S. Geological Survey aluminum leg bands and took the following standard morphological measurements: tarsus dorsal–ventral (smallest front to back measurement of the tarsus to nearest 0.1 mm), tarsus lateral (smallest side to side measurement of the tarsus to nearest 0.1 mm), hallux (tip of talon to the beginning of the fleshy pad of the hind toe to nearest 0.1 mm), bill depth (perpendicular to the bill from the top in front of the cere to the bottom of the bill to nearest 0.1 mm), culmen (top portion of the bill in front of the cere to the tip of the bill to nearest 0.1 mm), mass (taken to nearest 10 g). I used a *k*-means cluster analysis (SPSS 1997) to determine if morphological measurements could adequately identify sexes of nestlings. Only birds from broods in which all the measurements were collected were included in the analysis. In 1999, I collected blood samples from 22 nestlings and had them genetically analyzed for sex identification (Avian Biotech International, Tallahassee, FL U.S.A.) using a polymerase-chain reaction to amplify CHD (chromo-helicase-DNA binding) genes Z and W that are located on the avian sex chromosomes in birds. For detailed procedural information, see Griffiths et al. (1998), Fridolfsson

Table 1. Nestling sex-ratio and productivity of Northern Goshawks from territories monitored on the Apache-Sitgreaves National Forest, Arizona, (1993–98).

YEAR	NO. NESTS MONITORED	NESTING OCCUPANCY RATE ^a	NO. SUCCESSFUL BROODS	NO. MALE FLEDGLINGS	NO. FEMALE FLEDGLINGS	NO. FLEDGLINGS		SEX RATIO ^c	P ^d
						OF UNKNOWN SEX ^b			
1993	30	0.69	17	10	9	11		1.1	0.819
1994	33	0.33	8	9	3	4		3	0.083
1995	39	0.66	14	17	10	0		1.7	0.178
1996	42	0.52	16	16	8	4		2	0.102
1997	42	0.31	6	7	3	0		2.3	0.206
1998	44	0.43	15	17	10	3		1.7	0.178
Total	230	$\bar{x} = 0.49$	76	76	43	22		1.7	0.003

^a The number of occupied nests (a nest where at least one egg was laid)/total number of nesting territories monitored.

^b Fledglings not measured, therefore gender indeterminate.

^c Male/female.

^d Significance of Chi-square test for difference from a 1:1 sex ratio.

and Ellegren (1999), and Avian Biotech International (2005). I calculated the sex ratio as the number of male per female fledglings. I used a chi-square analysis to test if the sex ratio was significantly different from 1:1 (Zar 1984). I used Spearman's correlation analysis to test for significance in relationships between demographic parameters (e.g., sex ratio versus the number of territories with an occupied nest per the number of territories monitored). All statistical tests were deemed significant at $P < 0.05$, and all means were expressed $\pm 95\%$ Confidence Interval (CI). I compiled monthly summaries of total precipitation from U.S. National Oceanic and Atmospheric Administration records collected at the Show Low, Arizona, municipal airport (elevation = 1950 m) located within the study area.

RESULTS

Breeding territories were monitored over the 6-yr period (range = 30–44 per yr), yielding 109 nesting attempts and 141 fledglings produced from 76 successful broods (Table 1). Among the 63

broods from which gender could be determined, 29% fledged one young, 54% fledged two young, and 17% fledged three young (Table 2). Two relatively homogenous groups of nestlings were discerned using a *k*-means cluster analysis, and their morphological measurements showed minimal overlap (Table 3). The two groups are easily recognized when the lateral tarsus and culmen length measurements are plotted (Fig. 1). I considered all members of the larger group as females. The measurements used above correctly classified to gender all 22 nestlings that were genetically analyzed in 1999. The mean sex ratio across years was 1.93 ± 0.70 ($\pm 95\%$ CI) males/female (range = 1.1:1–3:1). When combining all fledglings of known sex (76 males and 43 females), a 1.77:1 male to female sex ratio resulted that was significantly different from 1:1 ($\chi^2 = 9.15$, $df = 1$, $P = 0.002$).

Table 2. Observed brood size and sex ratio of Northern Goshawks fledged on the Apache-Sitgreaves National Forest, Arizona, (1993–98).

NESTING OUTCOME	BROOD SIZE		
	1	2	3
All males	13	13	2
All females	5	7	0
1 male and 1 female	—	14	—
2 males and 1 female	—	—	8
1 male and 2 females	—	—	1
Sex ratio (M/F)	13/5 = 2.6	40/28 = 1.43	23/10 = 2.3
P ^a	0.06	0.15	0.02

^a Significance of Chi-square test for difference from a 1:1 sex ratio.

Table 3. Summary statistics of Northern Goshawk morphological measurements taken on the Apache-Sitgreaves National Forest, Arizona (1993–98).

GROUP	MEASUREMENT ($\bar{x} \pm 2$ SE, RANGE) ^a		
	FLEDGLING GROUP 1 (PRESUMED MALE)	FLEDGLING GROUP 2 (PRESUMED FEMALE)	ADULT FEMALES
	N = 59	N = 34	N = 25
Culmen (mm)	19.05 \pm 0.27 16.2–21.7	21.36 \pm 0.34 18.5–23.4	24.53 \pm 0.34 23.0–26.3
Beak depth (mm)	14.63 \pm 0.18 13.3–16.1	16.63 \pm 0.21 15.1–17.8	17.93 \pm 0.18 17.2–18.7
Tarsus D/V ^b (mm)	7.04 \pm 0.13 6.0–8.1	8.38 \pm 0.19 7.4–9.3	10.48 \pm 0.36 8.7–12.0
Tarsus L ^c (mm)	5.36 \pm 0.07 4.8–6.0	6.50 \pm 0.13 5.9–7.4	7.48 \pm 0.15 6.9–8.5
Hallux (mm)	23.79 \pm 0.36 19.6–27.0	27.02 \pm 0.52 24.1–31.1	31.98 \pm 0.39 30.2–33.8
Mass (g)	702 \pm 14 565–810	894 \pm 36 620–1085	1026 \pm 39 845–1265

^a See text for detailed description of measurements.

^b D/V = the smallest front to back measurement of the tarsus (dorsal/ventral).

^c L = the smallest side to side measurement of the tarsus (lateral).

DISCUSSION

Hypothesis 1—Nutritional Stress Would Minimize the Investment in Larger Sex. Meyers (1978) predicted that during periods of lower than average resource abundance, offspring sex ratio in a population should shift toward the sex having the lower energy needs. In times of plentiful resources, adults should invest in the larger offspring, which benefit from greater size. I observed a negative relationship between the annual sex ratio and the

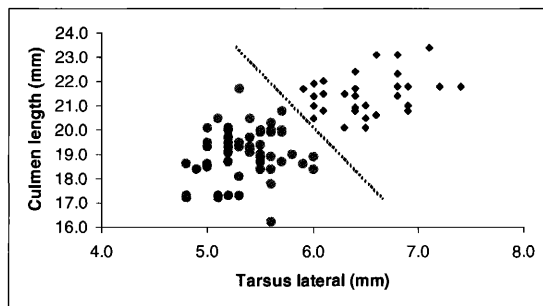


Figure 1. Plot of the culmen length and lateral tarsus measurements for Northern Goshawk nestlings measured on the Apache-Sitgreaves National Forest, AZ (1993–98). The two groups (circles presumed to be males and the diamonds females) were distinguished using a *k*-means cluster analysis of all morphological measurements collected.

nesting occupancy rate (Fig. 2A). A low nesting occupancy rate most likely reflects a lower than average abundance of some resource such as prey availability. Conversely, in years with a high nesting occupancy rate, which may have reflected an above average resource availability, the number of female offspring was greater (Fig. 2B). Yet, for this hypothesis to be an adaptive selection strategy, I would expect to find a sex ratio skewed toward females when the nesting occupancy was high. Instead when the nesting activity rate was high the sex ratio approached 1:1. This result may lend credence to the resource-shortage hypothesis being a nonadaptive by-product of differential mortality (Weatherhead and Teather 1991).

Hypothesis 2—Male Nestlings are Less Susceptible to Adverse Weather Conditions. Newton (1979) suggests that females would be more susceptible to mortality from exposure than smaller males. When being brooded, smaller nestlings may be more sheltered from environmental elements than larger siblings; or during episodes of rain, larger drenched female nestlings may hold more water and require more time to dry. Thus, larger female nestlings would remain cooler longer and be more susceptible to hypothermia. In years when more rainfall occurred during the nestling period (May and June), I observed more male fledglings

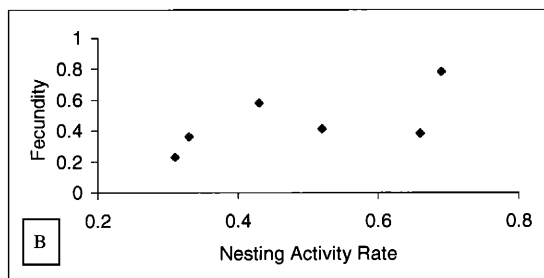
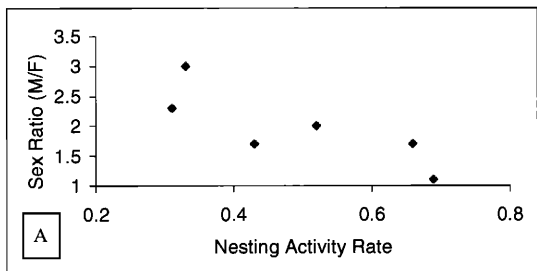


Figure 2. (A) Sex ratio of fledgling Northern Goshawks plotted against the annual nesting occupancy rate (number of occupied nests/total number of nests monitored) on the Apache-Sitgreaves National Forest, AZ, 1993–98 ($r = -0.84$, $P = 0.04$). (B) Fecundity rate (number of female fledglings produced/total number of breeding females) plotted against the nesting occupancy rate of Northern Goshawks on the Apache-Sitgreaves National Forest, AZ, 1993–98 ($r = 0.77$, $P = 0.07$).

produced (Fig. 3). This phenomenon of induced mortality due to exposure may also be compounded by nutritional stress (i.e., shortage of prey). Wet weather conditions have been shown to prevent adult raptors from hunting efficiently (Hiraldo et al. 1990, Kostrzewa and Kostrzewa 1990). Times of food shortage may force the nesting adult female to leave the nest in search of prey, thereby increasing the risk of exposure to the nestlings. For example, Boal et al. (2005) reported the failure of several nests in Minnesota after a 10-d period of constant rain.

CONCLUSION

I suggest that limited food availability combined with environmental stress in the form of exposure to the elements during a critical life stage (e.g., rainfall during the nesting stage) may be driving the skewed sex ratios observed in this local Northern Goshawk population. Of the two hypotheses

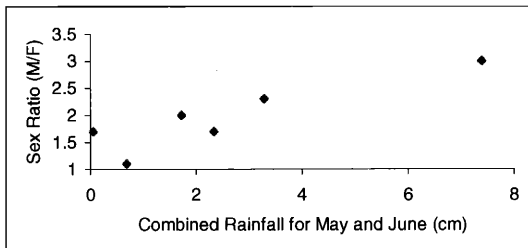


Figure 3. Relationship between the sex ratio of fledgling Northern Goshawks monitored from 1993–98 and rainfall ($r = 0.81$, $P = 0.05$) measured at the U.S. National Oceanic and Atmospheric Administration weather station located at the Show Low, Arizona, airport within the Apache-Sitgreaves National Forest, during the brood-rearing period (May and June).

presented, the available evidence supports that Northern Goshawks may exhibit selection toward the minimization of investment in the larger sex (i.e., support for the nutritional-stress hypothesis). But at this time the compounding phenomena of a potential increase in exposure time of nestlings because of the decrease in the adult female nest attentiveness due to a possible decrease in prey availability cannot be discarded. During the early nestling period, monitoring adult female nest attentiveness (i.e., her sheltering of the nestlings) and the amount of prey brought to the nestlings could help tease apart these two potential explanations that may be driving the skewed sex ratio (i.e., exposure or food shortage).

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