

DO SOME NORTHERN GOSHAWK NEST AREAS CONSISTENTLY FLEDGE MORE YOUNG THAN OTHERS?

ERICA L. McCLAREN^{1,3}, PATRICIA L. KENNEDY^{1,4} AND SARAH R. DEWEY²

¹Department of Fishery and Wildlife Biology, Colorado State University, Ft. Collins, CO 80523

²Bridger-Teton National Forest, Blackrock Ranger Station, P.O. Box 278, Moran, WY 83013

Abstract. In long-lived raptors, research suggests that some nest areas consistently fledge more young than others, with the majority of young in the population being produced by a few females. If this claim were true for Northern Goshawk (*Accipiter gentilis*) populations, it would benefit land managers to identify high-quality goshawk breeding habitat. We examined whether the number of young fledged varied spatially among Northern Goshawk nest areas within three study areas where long-term reproductive data from goshawks were available: (1) Vancouver Island, British Columbia; (2) Jemez Mountains, New Mexico; and (3) Uinta Mountains, Utah. A mixed-model ANOVA indicated there was minimal spatial variation in nest productivity among nest areas within the three study locations. Rather, nest areas exhibited high temporal variability in nest productivity within each study area. These results suggest that temporal patterns such as local weather and fluctuating prey populations influenced Northern Goshawk reproduction more than spatial patterns such as habitat characteristics. Nest productivity may inadequately reflect spatial patterns in goshawk reproduction and so it would be premature to assume that habitat quality for Northern Goshawks was equal among nest areas within these study areas. Future research should examine spatial variability among nest areas in adult and juvenile survival rates to gain a complete picture of population responses to habitat change.

Key words: *Accipiter gentilis* laingi, habitat quality, mixed models, nest productivity, reproduction, spatial variability, temporal variability.

¿Se Producen Consistentemente Más Volantones de *Accipiter gentilis* en Algunos Sitios de Anidación que en Otros?

Resumen. Investigaciones en aves rapaces longevas sugieren que consistentemente más polluelos empluman en algunos sitios de anidación que en otros y que la mayoría de los juveniles en la población son producidos por unas pocas hembras. Si esto fuera cierto para poblaciones de *Accipiter gentilis*, ayudaría a las autoridades ambientales a identificar hábitat reproductivo de alta calidad para la especie. Evaluamos si el número de polluelos emplumados varió espacialmente entre sitios de anidación de *A. gentilis* dentro de tres áreas de estudio para las cuales había datos reproductivos de largo plazo disponibles: (1) Vancouver Island, British Columbia; (2) Jemez Mountains, New Mexico; y (3) Uinta Mountains, Utah. Un modelo mixto de análisis de varianza indicó que la variación espacial en la productividad de los nidos entre sitios de anidación dentro de las tres áreas de estudio fue mínima. En cambio, los sitios de anidación presentaron una alta variabilidad temporal en la productividad de los nidos dentro de cada área de estudio. Estos resultados sugieren que los patrones temporales como el clima y las fluctuaciones de las poblaciones de presas influyen la reproducción de *A. gentilis* más que los patrones espaciales como las características del hábitat. La productividad de los nidos puede reflejar inadecuadamente los patrones espaciales de la reproducción de *A. gentilis*, de modo que sería prematuro suponer que la calidad de hábitat fue igual entre los sitios de anidación dentro de las áreas de estudio. Para tener una perspectiva completa de la respuesta de las poblaciones a cambios en el ambiente, investigaciones futuras deberían examinar la variabilidad espacial entre sitios de anidación en las tasas de supervivencia de aves adultas y juveniles.

INTRODUCTION

Research suggests that reproductive output varies among nest areas in long-lived birds; spe-

cifically some areas are occupied frequently and exhibit high nest productivity, and other areas are occupied inconsistently and fledge few young. Empirical work on Tengmalm's Owls (*Aegolius funereus*; Korpimäki 1988), Sparrowhawks (*Accipiter nisus*; Newton 1991), and Northern Goshawks (*Accipiter gentilis*, hereafter referred to as goshawk; Kostrzewa 1996) has led scientists to conclude that these patterns are influenced by variation in breeding habitat quality (Newton 1979, 1991, Kostrzewa 1996, Valkama

Manuscript received 22 May 2001; accepted 14 January 2002.

³ Present address: Ministry of Sustainable Resource Management, 2080A Labieux Road South, Nanaimo, BC V9T 6J9, Canada.

⁴ Corresponding author. Present address: Eastern Oregon Agricultural Research Center, Union Experiment Station, Oregon State University, P.O. Box E, 372 So. 10th St., Union, OR 97883. E-mail: pat.kennedy@orst.edu

and Korpimäki 1999, Franklin et al. 2000). Importantly, Newton and colleagues discovered that a few female Sparrowhawks contributed most of the young to their study population, and these individuals bred in the high-quality habitat (Newton 1989, 1991).

Habitat quality in birds is often attributed to the habitat characteristics around nest areas, because these influence predation levels (Carey et al. 1992), prey availability (Beier and Drennan 1997, Valkama and Korpimäki 1999), competition rates (Kostrzewa and Kostrzewa 1991), and nest-area microclimate (North et al. 2000). For raptors that breed and forage in mature and old-growth forests, it is frequently assumed that forest structure influences their reproduction and that individuals breeding in fragmented and young forests will have lower productivity than those breeding in contiguous stands of older forests (Redpath 1995, Patla 1997, Franklin et al. 2000). However, few researchers have been able to clearly demonstrate a link between vegetation and raptor reproduction, which would be important in understanding the influence of habitat alterations on raptor populations (Rodenhouse et al. 1997, Newton 1998, Thome et al. 1999). This research may be inconclusive because researchers seldom separate temporal and spatial components of variation and explicitly test for variation in reproduction among nest areas within their study population (goshawks: Woodbridge and Detrich 1994, Patla 1997; Spotted Owls [*Strix occidentalis*]: Meyer et al. 1998, North et al. 2000; Eurasian Kestrels [*Falco tinnunculus*]: Valkama and Korpimäki 1999). Rather, they define several vegetation attributes or landscape metrics and then try to link these directly to an assumed degree of variation in reproduction.

To assist scientists with separating natural levels of variation in raptor reproduction from human-induced levels of variation, we examined the degree of spatial and temporal variation in the number of goshawk fledglings per nest area within British Columbia, New Mexico, and Utah where nest productivity was monitored for 9–12 years. The status of goshawk populations in North America has been the center of debate among the public and scientists (Kennedy 1997, 1998, Crocker-Bedford 1998, DeStefano 1998, Smallwood 1998). This debate is spurred by the unknown effects of habitat alteration (i.e., forest harvest) on goshawk population persistence. Our results can provide a first step to help research-

ers clarify the demographic patterns in goshawks, particularly temporal and spatial variability in goshawk nest productivity as compared to other birds.

METHODS

STUDY AREAS

The three study areas were (1) Vancouver Island, British Columbia, Canada; (2) Jemez Mountains, New Mexico; and (3) Uinta Mountains, Utah. On Vancouver Island, nest areas were within forests dominated by western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*), although western redcedar (*Thuja plicata*), amabilis fir (*Abies amabilis*), and red alder (*Alnus rubra*) were also abundant. The terrain on Vancouver Island consists of rugged mountains dissected by many creek drainages. Elevations of nest areas ranged from 150–850 m. Mean daily temperatures range from 4.1°C in the winter (October to April) to 14.3°C in the summer (May through September), and mean monthly precipitation ranges from 40 mm (July) to 234 mm (December), with a mean annual total of 1409 mm, most of which falls as rain (Environment Canada 1998). In Utah, nest areas were primarily within lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), or mixed aspen-lodgepole pine forest types. Elevations of nest areas ranged from 2300–2800 m, and the average annual precipitation was 700 mm with precipitation resulting equally from winter snowfall and summer rains (for more details see Dewey and Kennedy 2001). Nest areas in New Mexico were located in ponderosa pine, Douglas-fir and white fir (*Abies concolor*) forest cover types. Elevations of nest areas ranged from 1645–3200 m and the average annual precipitation is 450 mm, 75% of which occurs from May through October (for more details see Siders and Kennedy 1996). We collected data from 1991–2000 ($n = 13$ nest areas) in British Columbia, from 1984–1995 ($n = 16$) in New Mexico, and from 1991–1999 ($n = 24$) in Utah (Table 1).

DATA COLLECTION

The unit of analysis in this study was the nest area. We defined nest area as the component of a goshawk's home range that was occupied by one breeding pair during each breeding season. Nest areas contained multiple alternative nest trees, which received variable usage by gos-

TABLE 1. Number of years that Northern Goshawk nest productivity data were collected and nest areas were monitored in British Columbia, New Mexico, and Utah. Nest areas with fewer than three years of nest productivity data were not included.

Study area	Nest area	Number of years		Years	
		Nest productivity	Nest monitoring		
British Columbia	Cervus	4	6	1995–2000	
	Claud	4	5	1996–2000	
	Cotton	3	4	1997–2000	
	Derby	4	5	1996–2000	
	Klak	3	5	1996–2000	
	Loon	4	7	1994–2000	
	Lukwa	4	5	1996–2000	
	Lupin	5	6	1995–2000	
	McLaugh	5	9	1991–2000	
	Paterson	6	6	1995–2000	
	Tlatlos	3	7	1994–2000	
	Tsitika	4	7	1994–2000	
	Vernon	3	4	1997–2000	
	New Mexico	Baca	5	7	1989–1995
		Barley	4	4	1992–1995
CerroP1		4	4	1992–1995	
CerroP2		4	6	1990–1995	
CerroPav		4	4	1992–1995	
Garcia		7	9	1987–1995	
Golondri		4	5	1991–1995	
Guaje		8	9	1987–1995	
Horsehoe		9	10	1984–1995	
LasConc		3	4	1992–1995	
MesaAlta		4	4	1992–1995	
MesaGuru		3	4	1992–1995	
Pajarito		9	11	1984–1995	
Pony		3	5	1991–1995	
Redondo		5	11	1984–1995	
Telephone		4	5	1991–1995	
Utah		Allen	3	5	1995–1999
		Burnt	5	8	1992–1999
	Center	8	9	1991–1999	
	Cub	9	9	1991–1999	
	DryGulch	5	9	1991–1999	
	DyerPk	3	9	1991–1999	
	EFEagle	4	7	1993–1999	
	EastMck	4	8	1992–1999	
	ElkPk	7	8	1992–1999	
	Green	4	8	1992–1999	
	Lodgepole	8	9	1991–1999	
	LowerGr	5	6	1994–1999	
	MillPk	4	7	1993–1999	
	MoonLk	8	8	1992–1999	
	Mosby	3	6	1994–1999	
	NFSheep	3	9	1991–1999	
	Pole	5	5	1995–1999	
	SinkR	3	4	1996–1999	
	Skull	4	8	1992–1999	
	Snowpole	3	4	1996–1999	
SouthAnd	6	9	1991–1999		
WFEagle	6	9	1991–1999		
Whiskey	5	8	1992–1999		
Yellow	3	8	1992–1999		

hawks throughout the years we monitored nest productivity (Reynolds et al. 1992). Goshawk nest-area size varies and depends on the topography and availability of suitable nest trees (Reynolds et al. 1992). On average, alternative nest trees in nest areas are within 300 m of each other (Squires and Reynolds 1997). Table 1 lists the number of years that nest productivity data were collected at each of the 53 nest areas.

In New Mexico and Utah we located active goshawk nest trees by broadcasting goshawk calls throughout forests of various age and species composition, following methods outlined by Kennedy and Stahlecker (1993). In British Columbia, these methods were modified to include broadcasting three sets of calls (rather than six), spacing broadcast stations and transect lines 400 m apart (rather than spacing stations 300 m apart and transects 260 m apart), and listening for 5 min at the end of broadcast calls for a goshawk detection (rather than 30 sec, McClaren 2001). These modifications were intended to improve the efficacy and efficiency of broadcast surveys in steep terrain and dense, coastal forests (Resource Inventory Committee 1997). Forest company personnel, Forest Service personnel, and the public opportunistically located some of the goshawk nest trees in the three study areas. We determined activity each year by visiting known nest trees within nest areas during the incubation period (late April–May). If we did not observe an incubating female at known nest trees, we returned during the nestling (June) and fledgling-dependency (early July–early August) periods to broadcast adult alarm and juvenile begging calls, respectively. In New Mexico and Utah, broadcast surveys occurred within a 0.7–1.0-km-radius area centered on the previously active nest. In British Columbia, broadcast surveys occurred within a 1.6-km-radius of the previously active nest. The area surveyed to locate active goshawk nests in British Columbia was larger than in New Mexico and Utah because alternative nest trees within nest areas tend to be more widely spaced in coastal forests (Iverson et al. 1996).

We used the number of young fledged per active nest area as our measure of goshawk reproduction, instead of nest initiation rates or clutch size, due to the difficulties associated with detecting goshawks and locating active nest trees before their young have hatched (Kennedy and Stahlecker 1993, McClaren 2001). Once we lo-

cated the active nest tree within nest areas each year, we defined the number of fledglings as the number of young observed in the nest approximately one week prior to fledging (32–40 days). We estimated nest productivity just prior to fledging rather than after fledging since birds are easily missed after they fledge (Steenhof 1987). We recognize nests that failed early in the season may have been missed, leading to inflated estimates of the number of young fledged per active nest area (Steenhof 1987). However, by monitoring a number of known nest areas over time, we maximized our likelihood of finding active nest trees early in the season. When nests failed, they were included in our analyses as fledging zero young. We also considered nest areas where a goshawk pair was observed defending in May or June, but neither an active nest tree nor fledglings were observed, as active but failing to fledge young. Active nest trees that were used as treatments (i.e., provided with food) in food supplementation experiments conducted by Ward and Kennedy (1996) in New Mexico and Dewey and Kennedy (2001) in Utah were not included in these analyses.

STATISTICAL ANALYSES

To maintain consistency among the methods used in each study area, we excluded nest areas from analyses when the protocols described above were not followed. Bias introduced from variation in observer skill was minimized in each study area because the same observer was present throughout years during which nest areas were monitored (British Columbia = ELM, New Mexico = PLK, Utah = SRD). We did not want habitat modifications around monitored nest areas to confound our results. Consequently, we omitted nest areas where human-induced habitat modifications (i.e., logging) occurred <200 m from active nest trees, unless three years of data were available pre- and post-disturbance ($n = 1$). For the one nest area where sufficient pre- and post-disturbance breeding data were available, we renamed the nest area post-disturbance and included it in the analysis as two different nest areas. Thus, the habitat characteristics around nest areas during our study were treated as static within the scale of our analysis, rather than changing through time.

Spatial and temporal variation in nest productivity within study areas. We used a mixed-model ANOVA (PROC MIXED; Littell et al.

1996) to examine the variability in number of young fledged among nest areas within each study area. Year was the fixed effect, whereas nest area and nest area \times year interaction were random effects. Treating nest area as a random effect assumes that nest areas were randomly sampled from a population of goshawk nest areas and thereby extends our level of inference to the population of nesting areas within each study area, rather than limiting it to our samples. We used PROC GLM (SAS Institute, Inc. 1997) with the *random* statement to generate the appropriate *F*-tests for nest area because *F*-tests generated by PROC MIXED for random effects are inaccurate (P. L. Chapman, Statistics Department, Colorado State University, pers. comm.). Year \times nest area interaction was not estimable in our models because there were too few degrees of freedom for the test. Because goshawks do not nest every year (Squires and Reynolds 1997), and because we intended to measure temporal trends in nest productivity, we considered fewer than three years of data per nest area to be insufficient for inclusion in this analysis.

Comparison among study areas. To determine if temporal patterns in nest productivity were similar among study areas, we compared the mean number of young fledged year⁻¹ among the three study areas using ANOVA (PROC GLM; SAS Institute, Inc. 1997). In these models, study area was the class variable and number of young fledged was the response variable. Only those years in which nest productivity data were collected for the same years were compared. We did not restrict our analyses of mean annual nest productivity per study area to those nest areas where at least three years of data were available because we were examining differences in nest productivity for a snapshot in time. When the mean number of young fledged differed greatly ($P < 0.05$) among study areas for a given year, we used least-squares means (PROC GLM; SAS Institute, Inc. 1997) to conduct pairwise comparisons between study areas. When productivity data were collected in only two study areas for a given year, Wilcoxon rank-sum tests (PROC NPAR1WAY; SAS Institute, Inc. 1997) were used for pairwise comparisons between study areas for the mean number of young fledged year⁻¹. We used Wilcoxon rank-sum tests for pairwise comparisons because unequal sample sizes and nonnormal data may in-

validate the results provided by *t*-tests (Ott 1993). However, we used ANOVA to compare three means because the assumptions of ANOVA are more robust to nonnormality in the data than *t*-tests (Ott 1993). We validated the homogeneity of variance assumption for ANOVA tests with predicted-studentized residual plots.

To reduce the influence of sample-size differences among study areas on comparisons of mean annual nest productivity, only those years where at least five nest areas were active per study area were included in the above analyses. As well, we tested for a correlation between the number of active nest areas per study area and mean number of young fledged using PROC CORR (SAS Institute, Inc. 1997). All analyses were conducted using SAS Version 7.0.

RESULTS

SPATIAL VARIATION IN NEST PRODUCTIVITY

Overall, there was minimal spatial variability in the number of young fledged among goshawk nest areas within each study location (British Columbia: $s^2 = 0.01$, New Mexico: $s^2 = 0.05$, Utah: $s^2 = 0.04$). This suggested that goshawk nest areas had little influence on the number of young fledged in British Columbia ($F_{12,32} = 1.0$; $P = 0.5$), New Mexico ($F_{15,53} = 1.4$; $P = 0.2$), and Utah ($F_{23,86} = 1.2$; $P = 0.3$; Fig. 1). Although nest area was not statistically significant, 1–2 nest areas within each study area appeared to consistently fledge more young than others (Fig. 1). In particular, Loon (British Columbia), Lupin (British Columbia), LasConc (New Mexico), and Allen (Utah) tended to be highly productive.

TEMPORAL VARIATION IN NEST PRODUCTIVITY

The number of young fledged per nest area varied greatly among years in each study area (British Columbia: $F_{7,40} = 5.5$, $P < 0.001$; New Mexico: $F_{11,59} = 4.1$, $P < 0.001$; Utah: $F_{8,100} = 5.1$, $P < 0.001$; Fig. 2). Some years seemed to be “good” for goshawk nest productivity, whereas others seemed to be “poor.” In British Columbia, mean nest productivity ranged from 0.7 (1999) to 2.4 (1994) fledglings per nest area and was particularly high in 1994, 2000, and 1998. In New Mexico, the mean number of young fledged ranged from 0.5 (1993) to 2.1 (1992) and peaked in 1992, 1991, and 1995. Mean nest productivity ranged from 0.4 (1998) to 2.3

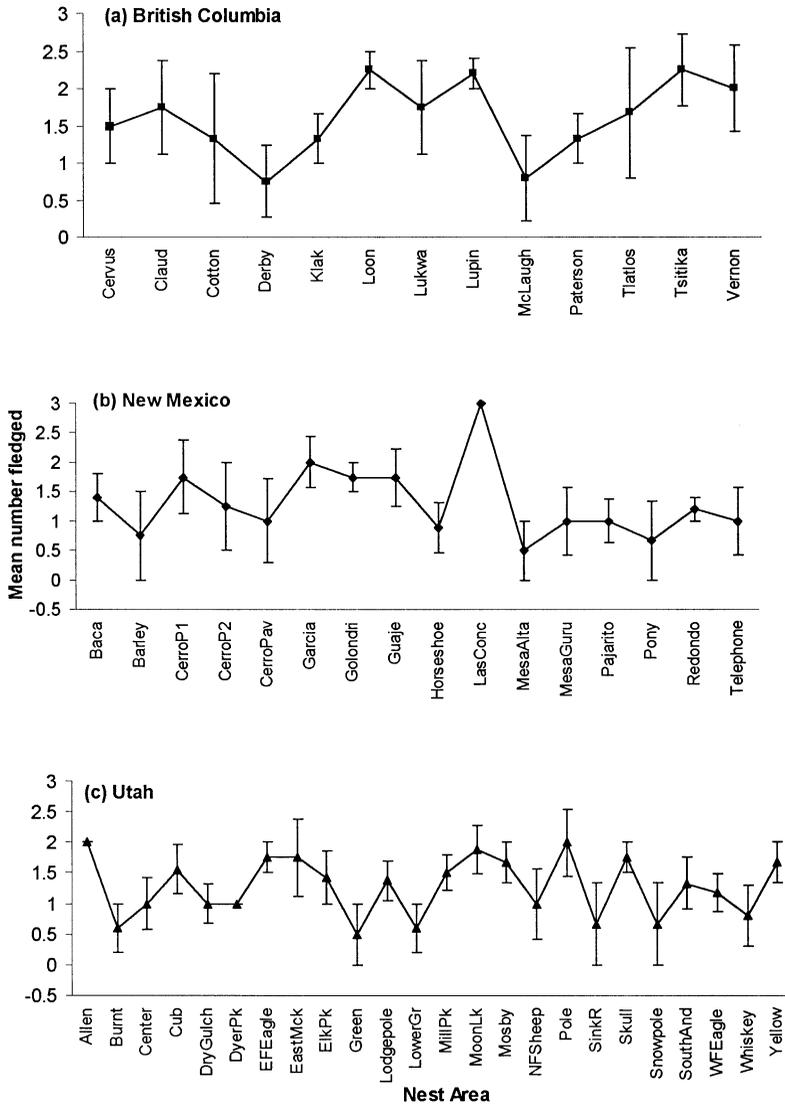


FIGURE 1. Spatial variation (mean \pm SE) in the number of young fledged among goshawk nest areas within: (a) British Columbia; (b) New Mexico; and (c) Utah. Only nest areas with ≥ 3 years of reproductive data are included.

(1996) in Utah, and peak years were 1996, 1992, and 1995.

COMPARISON AMONG STUDY AREAS

Years of high nest productivity for goshawks in British Columbia did not coincide with years of high nest productivity for goshawks in New Mexico and Utah. For example, in 1994, the mean number of young fledged per nest area was higher in British Columbia than in New Mexico and Utah ($F_{2,34} = 5.5, P = 0.01$; Fig. 2). In 1996,

goshawks nesting in Utah fledged more young than in British Columbia ($S = 237, P = 0.08$) whereas this pattern was reversed in 1998 ($S = 188, P < 0.001$; Fig. 2). Insufficient data were available for British Columbia from 1991–1993, New Mexico from 1996–2000, and Utah for 2000. Throughout the study periods, mean \pm SE nest productivity for all nest areas in British Columbia was 1.6 ± 0.2 ($n = 51$), 1.3 ± 0.1 ($n = 118$) within Utah, and 1.3 ± 0.1 ($n = 80$) within New Mexico.

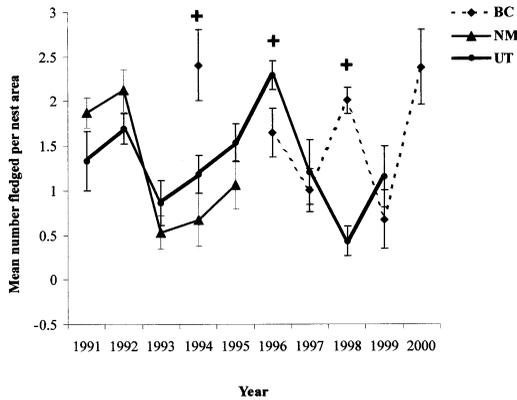


FIGURE 2. Temporal variation (mean \pm SE) in the number of goshawk young fledged per nest area within British Columbia (BC), New Mexico (NM), and Utah (UT). Data are presented only for periods when at least two regions sampled goshawk productivity. +Indicates statistical differences among regions of $P < 0.1$.

In all study areas the mean number of young fledged year⁻¹ had no relationship to the number of active nest areas year⁻¹ (British Columbia: $r = -0.3$, $P = 0.6$; New Mexico: $r = -0.5$, $P = 0.4$; Utah: $r = 0.02$, $P = 1.0$). If the statistical power of this test was adequate (an untested assumption), these differences among study areas in mean nest productivity were not merely reflections of differences in the number of active nest areas study area⁻¹ year⁻¹.

DISCUSSION

SPATIAL VARIATION IN GOSHAWK NEST PRODUCTIVITY

We found surprisingly low spatial heterogeneity in the number of young fledged among goshawk nest areas within each of three study areas in a variety of vegetation types in western North America. Few studies have explicitly examined spatial variability in avian reproduction, and the results are equivocal. Our results concur with a study on a German population of goshawks where nest productivity did not vary significantly among groups of nest areas classified as low, medium, and high quality based on occupancy rates (Krüger and Lindström 2001). However, Krüger and Lindström (2001) reported that brood size significantly differed among low, medium, and high occupancy nest areas. Similarly, McCarty (2001) reported little spatial variation in nest productivity between two proximal populations of Tree Swallows (*Tachycineta bicolor*)

in New York, although nestling growth rates were significantly greater at one site than at the other. Conversely, significant spatial variation in nest productivity has been documented among Black-legged Kittiwake (*Rissa tridactyla*) breeding colonies in Alaska (Suryan and Irons 2001) and Northern Spotted Owl (*Strix occidentalis caurina*) nest areas in California (Franklin et al. 2000).

We may have observed low spatial variation in goshawk nest productivity because only those nest areas where pairs were present and initiated breeding were included in our analyses. Therefore, we may have inadvertently included only individuals on nest areas where breeding conditions were favorable and missed those where nest areas were unsuitable for breeding. In those areas individuals may have abandoned early and not proceeded from courtship to egg laying. For example, 6, 11, and 23 nest areas in British Columbia, New Mexico, and Utah, respectively, were active at least once during the years we monitored them but were not included in our analyses because they did not have at least three years of nest productivity data. Suryan and Irons (2001) and Dreitz et al. (2001) have expressed similar concerns with using nest productivity to examine spatial variation among breeding sites.

Spatial variation in nest initiation rates may more accurately reflect nest area habitat quality. However, nest initiation rates are problematic to estimate for secretive species such as goshawks (Steenhof 1987). Nonetheless, lower occupancy and higher desertion rates on low-quality territories compared to high-quality territories have been observed for several raptor species (Tengmalm's Owls, Korpimäki 1988; Sparrowhawks, Newton and Marquiss 1991; Tawny Owls [*Strix aluco*], Redpath 1995; goshawks, Kostrzewa 1996).

Comparing nest productivity among birds of unknown age has also been criticized because older individuals in long-lived species often produce more young, regardless of habitat quality (Newton 1991, 1998, Koenig et al. 1992). This concern is relevant when older individuals are randomly distributed throughout high and low-quality nest areas. However, most long-term studies on raptors have observed older birds occupying the high-quality habitat (Moore and Henny 1984, Newton 1991, Newton and Rothery 1997), inflating rather than diminishing differences among nest areas that result from in-

dividual age. Furthermore, the relationship between parental age and the number of young fledged pair⁻¹ remains unclear for goshawks (Younk and Bechard 1994, Reynolds et al. 1994). Very few individuals breeding in British Columbia, Utah, and New Mexico were in juvenile or subadult plumage, suggesting age might not have influenced the patterns we observed. However if goshawk reproductive output varies at finer scales than subadult and adult classifications, then individual age may have confounded our results.

TEMPORAL VARIATION IN GOSHAWK NEST PRODUCTIVITY

Our results suggest there is strong annual variability in nest productivity within nest areas and the temporal pattern is not consistent across study areas. High temporal variation in nest productivity has been observed in several bird species, and most often these patterns result from variation in local weather and prey availability (Snail Kites [*Rostrhamus sociabilis*], Dreitz et al. 2001; Tree Swallows, McCarty 2001; Black-legged Kittiwakes, Suryan and Irons 2001).

In general, goshawk productivity is negatively impacted by high levels of spring precipitation, and warm spring temperatures favor goshawk reproduction (Kostrzewa and Kostrzewa 1990, 1991, Penteriani 1997, Patla 1997). During courtship, it is important for male raptors to provide females with sufficient food for them to obtain the critical body mass required for egg laying (Newton 1986, Korpimäki 1990). High rainfall during this time may limit the male's foraging opportunities and hunting success. In incubation and the early nestling phase, low temperatures and high rainfall may chill eggs and chicks, and result in addled eggs, retarded chick growth, or chick mortality (Kostrzewa and Kostrzewa 1990).

Annual fluctuations in prey populations may also create high temporal variability in nest productivity among goshawk nest areas. In New Mexico (Ward and Kennedy 1996) and Utah (Dewey and Kennedy 2001), food supplementation experiments at goshawk nests increased nestling survival in some years but not in others. The authors attributed this variation in nestling survival to fluctuations in natural food levels, with food supplementation being less effective in years when prey populations were naturally high relative to years with low prey availability.

Correlative evidence from North America and Europe suggests that goshawk reproduction may be related to the abundance of cyclic prey populations (Lindén and Wikman 1983, Doyle and Smith 1994), primarily snowshoe hare (*Lepus americanus*) and grouse.

Prey levels may also indirectly influence nest productivity by affecting the time adult females allocate to nest defense or foraging, which may also influence the occurrence of predation, cannibalism, and siblicide at nests (Boal and Bacorn 1994, Ward and Kennedy 1996, Dewey and Kennedy 2001). It appears that where nest predation is prevalent in goshawk nest areas, abundant food supplies will increase breeding success by reducing both starvation and predation of nestlings (Ward and Kennedy 1996, Dewey and Kennedy 2001). Weather and prey population levels were not measured in British Columbia, New Mexico, or Utah. Thus, we can only speculate that these factors account for much of the temporal variation we observed in nest productivity.

Few goshawk nest areas within British Columbia, New Mexico, and Utah consistently fledged more young than others over the years we monitored them. Rather, there was large annual variability in nest productivity within each nest area. Because nest areas where birds failed to lay eggs were not included in this study, nest productivity may inaccurately reflect spatial variation in reproduction among nest areas. However, we should continue to monitor the presence or absence of breeding goshawks within nest areas as the surrounding landscapes continue to change, even though determining the absence of breeding goshawks requires much effort (Kennedy and Stahlecker 1993, McClaren 2001). Both DeStefano (1998) and Kennedy (1998) recommend using landscape manipulations as on-site experiments to measure goshawk demographic responses to silvicultural treatments.

When assessing habitat quality for birds it is essential to also examine spatial variability in adult and fledgling survival rates, as both reproduction and survival ultimately determine an individual's fitness (Newton 1989, Stearns 1992, Franklin 1997). Failing to do this may lead land managers to draw incorrect conclusions regarding goshawk habitat requirements (Hall et al. 1997).

ACKNOWLEDGMENTS

We thank T. Ethier for initiating the goshawk project on Vancouver Island and we are grateful to D. Doyle for his feedback and his aptitude at securing funds. We thank K. Paulin for her vision in getting the goshawk-monitoring project off the ground in Utah, and her long-standing and continued support of our research and monitoring efforts. We appreciate the hard work and dedication of the many field assistants who collected nest productivity data. In particular, we thank M. Bigg, D. Cator, D. Klinka, D. Koshowski, M. McAdie, S. McDonald, S. Pendegast, G. Schreiber, K. Wickert, and A. Zeeman (British Columbia); J. Cook, J. Cropley, W. Estes, M. Estrella, D. Kipervaser, S. Lewis, T. Morris, C. Nielsen, L. Ortiz, M. Painter, S. Rayroux, S. Rutherford, D. Sedlachek, and G. Socha (Utah); T. Dean, V. Dreitz, J. Morrison, M. Siders, D. Sinton, and J. Ward (New Mexico). We are indebted to G. White for his statistical wisdom and for setting us on the right track with this analysis. We thank Forest Renewal British Columbia for funding this project and Weyerhaeuser, TimberWest, CANFOR, and Western Forest Products for their cooperation and support. K. Wilson, M. Baker, B. Van Horne, and two anonymous reviewers provided insightful comments on earlier drafts of this manuscript.

LITERATURE CITED

- BEIER, P., AND J. E. DRENNAN. 1997. Forest structure and prey abundance in foraging areas of Northern Goshawks. *Ecological Applications* 7:564–571.
- BOAL, C. W., AND J. E. BACORN. 1994. Siblingicide and cannibalism at Northern Goshawk nests. *Auk* 111:748–750.
- CAREY, A. B., S. P. HORTON, AND B. L. BISWELL. 1992. Northern Spotted Owls: influence of prey base and landscape characteristics. *Ecological Monographs* 62:223–250.
- CROCKER-BEDFORD, D. C. 1998. The value of demographic and habitat studies in determining the status of Northern Goshawks (*Accipiter gentilis atricapillus*) with special reference to Crocker-Bedford (1990) and Kennedy (1997). *Journal of Raptor Research* 32:329–335.
- DESTEFANO, S. 1998. Determining the status of Northern Goshawks in the west: is our conceptual model correct? *Journal of Raptor Research* 32:342–348.
- DEWEY, S. R., AND P. L. KENNEDY. 2001. Effects of supplemental food on parental-care strategies and juvenile survival of Northern Goshawks. *Auk* 118:352–365.
- DOYLE, F. I., AND J. M. N. SMITH. 1994. Population responses of Northern Goshawks to the 10-year cycle in numbers of snowshoe hares. *Studies in Avian Biology* 16:122–129.
- DREITZ, V. J., R. E. BENNETTS, B. TOLAND, W. M. KITCHENS, AND M. W. COLLOPY. 2001. Spatial and temporal variability in nest success of Snail Kites in Florida: a meta-analysis. *Condor* 103:502–509.
- ENVIRONMENT CANADA [ONLINE]. 1998. Canadian climate normals 1961–1990: Campbell River airport, British Columbia. (<http://www.cmc.ec.gc.ca/climate/normal/British ColumbiaC002.htm>) (29 March 2000).
- FRANKLIN, A. B. 1997. Factors affecting temporal and spatial variation in Northern Spotted Owl populations in northwest California. Ph.D. dissertation, Colorado State University, Ft. Collins, CO.
- FRANKLIN, A. B., D. R. ANDERSON, R. J. GUTIÉRREZ, AND K. P. BURNHAM. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecological Monographs* 70:539–590.
- HALL, L. S., P. R. KRAUSMAN, AND M. L. MORRISON. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25:173–182.
- IVERSON, G. C., G. D. HAYWARD, K. TITUS, E. DEGAYNER, R. E. LOWELL, C. D. CROCKER-BEDFORD, F. P. SCHEMPF, F. PHILIP, AND J. LINDELL. 1996. Conservation assessment of the Northern Goshawk in southeast Alaska. USDA Forest Service General Technical Report PNW-GTR-387.
- KENNEDY, P. L. 1997. The Northern Goshawk (*Accipiter gentilis atricapillus*): is there evidence of a population decline? *Journal of Raptor Research* 31:95–106.
- KENNEDY, P. L. 1998. Evaluating Northern Goshawk (*Accipiter gentilis atricapillus*) population trends: a reply to Smallwood and Crocker-Bedford. *Journal of Raptor Research* 32:336–341.
- KENNEDY, P. L., AND D. W. STAHLCKER. 1993. Responsiveness of nesting Northern Goshawks to taped broadcasts of 3 conspecific calls. *Journal of Wildlife Management* 57:249–257.
- KOENIG, W. D., F. A. PITELKA, W. J. CARMEN, R. L. MUMME, AND M. T. STANBACK. 1992. The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* 67:111–150.
- KORPIMÄKI, E. 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's Owl. *Journal of Animal Ecology* 57:97–108.
- KORPIMÄKI, E. 1990. Body mass of breeding Tengmalm's Owls *Aegolius funereus*: seasonal, between-year, site and age-related variation. *Ornis Scandinavica* 21:169–178.
- KOSTRZEWA, A. 1996. A comparative study of nest-site occupancy and breeding performance as indicators for nesting-habitat quality in three European raptor species. *Ethology, Ecology and Evolution* 8:1–18.
- KOSTRZEWA, A., AND R. KOSTRZEWA. 1990. The relationship of spring and summer weather with density and breeding performance of the Buzzard *Buteo buteo*, Goshawk *Accipiter gentilis* and Kestrel *Falco tinnunculus*. *Ibis* 132:550–559.
- KOSTRZEWA, R., AND A. KOSTRZEWA. 1991. Winter weather, spring and summer density, and subsequent breeding success of Eurasian Kestrels, Common Buzzards, and Northern Goshawks. *Auk* 108:342–347.
- KRÜGER, O., AND J. LINDSTRÖM. 2001. Habitat heterogeneity affects population growth in goshawk *Accipiter gentilis*. *Journal of Animal Ecology* 70:173–181.

- LINDÉN, H., AND M. WIKMAN. 1983. Goshawk predation on tetraonids: availability of prey and diet of the predator in the breeding season. *Journal of Animal Ecology* 52:953–968.
- LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute, Cary, NC.
- MCCARTY, J. P. 2001. Variation in growth of nestling Tree Swallows across multiple temporal and spatial scales. *Auk* 118:176–190.
- MCCLAREN, E. L. 2001. Factors influencing Northern Goshawk detectability and reproduction on Vancouver Island, British Columbia. M.Sc. thesis, Colorado State University, Ft. Collins, CO.
- MEYER, J. S., L. L. IRWIN, AND M. S. BOYCE. 1998. Influence of habitat abundance and fragmentation on Northern Spotted Owls in western Oregon. *Wildlife Monographs* 139:1–51.
- MOORE, K. R., AND C. J. HENNY. 1984. Age-specific productivity and nest site characteristics of Cooper's Hawks (*Accipiter cooperii*). *Northwest Science* 58:290–299.
- NEWTON, I. 1979. Population ecology of raptors. Poyser, Berkhamsted, UK.
- NEWTON, I. 1986. The Sparrowhawk. Poyser, Calton, UK.
- NEWTON, I. 1989. Sparrowhawk, p. 279–296. *In* I. Newton [ED.], Lifetime reproduction in birds. Academic Press Ltd., London.
- NEWTON, I. 1991. Habitat variation and population regulation in Sparrowhawks. *Ibis* 133(Suppl. 1):76–88.
- NEWTON, I. 1998. Population limitation in birds. Academic Press Ltd., London.
- NEWTON, I., AND M. MARQUISS. 1991. Removal experiments and the limitation of breeding density in Sparrowhawks. *Journal of Animal Ecology* 60:535–544.
- NEWTON, I., AND P. ROTHERY. 1997. Senescence and reproductive value in Sparrowhawks. *Ecology* 78:1000–1008.
- NORTH, M., G. STEGER, R. DENTON, G. EBERLEIN, T. MUNTUN, AND K. JOHNSON. 2000. Association of weather and nest-site structure with reproductive success in California Spotted Owls. *Journal of Wildlife Management* 64:797–807.
- OTT, R. L. 1993. An introduction to statistical methods and data analysis, 4th ed. Duxbury Press, Belmont, CA.
- PATLA, S. 1997. Nesting ecology and habitat use of the Northern Goshawk in undisturbed and timber harvest areas on the Targhee National Forest, Greater Yellowstone Ecosystem. M.Sc. thesis, Idaho State University, Pocatello, ID.
- PENTERIANI, V. 1997. Long-term study of Goshawk breeding population on a Mediterranean mountain (Abruzzi Apennines, central Italy): density, breeding performance and diet. *Journal of Raptor Research* 31:308–312.
- REDPATH, S. M. 1995. Habitat fragmentation and the individual: Tawny Owls *Strix aluco* in woodland patches. *Journal of Animal Ecology* 64:652–661.
- RESOURCE INVENTORY COMMITTEE. 1997. Standard inventory methodologies for components of British Columbia's biodiversity: raptors. Version 1.1. Ministry of Environment, Lands and Parks, Wildlife Branch, Victoria, BC, Canada.
- REYNOLDS, R. T., R. T. GRAHAM, M. H. REISER, R. L. BASSETT, P. L. KENNEDY, D. A. BOYCE, G. GOODWIN, R. SMITH, AND E. L. FISHER. 1992. Management recommendations for the Northern Goshawk in the southwestern United States. USDA Forest Service General Technical Report RM-GTR-217.
- REYNOLDS, R. T., S. M. JOY, AND D. G. LESLIE. 1994. Nest productivity, fidelity and spacing of Northern Goshawks in northern Arizona. *Studies in Avian Biology* 16:106–113.
- RODENHOUSE, N. L., T. W. SHERRY, AND R. T. HOLMES. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* 78:2025–2042.
- SAS INSTITUTE INC. 1997. SAS/STAT Software: changes and enhancements through release of 6.12. SAS Institute Inc., Cary, NC.
- SIDERS, M. S., AND P. L. KENNEDY. 1996. Forest structural characteristics of *Accipiter* nesting habitat: is there an allometric relationship? *Condor* 98:123–132.
- SMALLWOOD, K. S. 1998. On the evidence needed for listing Northern Goshawks (*Accipiter gentilis*) under the Endangered Species Act: a reply to Kennedy. *Journal of Raptor Research* 32:323–328.
- SQUIRES, J. R., AND R. T. REYNOLDS. 1997. Northern Goshawk (*Accipiter gentilis*), p. 1–32. *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 298. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- STEARNS, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.
- STEENHOF, K. 1987. Assessing raptor reproductive success and productivity, p. 157–170. *In* B. A. Giron Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird [EDS.], Raptor management techniques manual. Scientific and Technical Series No. 10, National Wildlife Federation, Washington, DC.
- SURYAN, R. M., AND D. B. IRONS. 2001. Colony and population dynamics of Black-legged Kittiwakes in a heterogeneous environment. *Auk* 118:636–649.
- THOME, D. M., C. J. ZABEL, AND L. V. DILLER. 1999. Forest stand characteristics and reproduction of Northern Spotted Owls in managed north-coastal California forests. *Journal of Wildlife Management* 63:44–59.
- VALKAMA, J., AND E. KORPIMÄKI. 1999. Nestbox characteristics, habitat quality and reproductive success of Eurasian Kestrels. *Bird Study* 46:81–88.
- WARD, J. M., AND P. L. KENNEDY. 1996. Effects of supplemental food on size and survival of juvenile Northern Goshawks. *Auk* 113:200–208.
- WOODBIDGE, B., AND P. J. DETRICH. 1994. Territory occupancy and habitat patch size of Northern Goshawks in the southern Cascades of California. *Studies in Avian Biology* 16:83–87.
- YOUNK, J. V., AND M. J. BECHARD. 1994. Breeding ecology of the Northern Goshawk in high elevation forests of northern Nevada. *Studies in Avian Biology* 16:112–121.