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A REVIEW AND EVALUATION OF FACTORS LIMITING NORTHERN GOSHAWK POPULATIONS

Richard T. Reynolds, J. David Wiens, and Susan R. Salafsky

Abstract. Northern Goshawk (*Accipiter gentilis*) populations are suspected of declining due to forest-management treatments that alter the range of environmental conditions beneficial to their reproduction and survival. To develop effective goshawk conservation strategies, information on intrinsic and extrinsic factors that influence goshawk fitness is required. We reviewed the literature for information on factors that commonly limit avian populations, and were, therefore, potentially limiting goshawk populations. We evaluated the relative importance of these factors, and discussed how and at what scale these factors operate to constrain goshawk populations. Food availability and forest structure appeared to be the most ubiquitous factors limiting goshawks, but the degree to which these factors affected goshawks appeared to depend on interactions with other limiting factors such as weather, predation, competition, and disease, each of which operates at multiple spatial and temporal scales. Goshawks occur primarily in forests and woodlands, but the degree to which they are limited by forest composition and structure is difficult to determine because goshawks, at both the individual and population levels, use a wide variety of structural conditions while foraging. Much of the diversity in habitats used by hunting goshawks appears to result from their entry into the diverse habitats of their prey. Our review suggested that the availability of suitable nest sites influences goshawk site occupancy and reproduction, but that forest structural conditions beyond nest sites have a larger effect on goshawk reproduction and survival by affecting both the abundance and accessibility of their prey. This highlights the importance of conservation strategies that address a range of ecosystem needs by integrating the diverse habitat requirements of the goshawk prey community with the forest structural components of goshawk nest sites and foraging areas.

Key Words: *Accipiter gentilis*, competition, disease, food abundance and availability, forest composition and structure, Northern Goshawk, population limitation, predation, weather.

REVISIÓN Y EVALUACIÓN DE LOS FACTORES QUE LIMITAN A LAS POBLACIONES DE GAVILÁN AZOR

Resumen. Se sospecha que las poblaciones del Gavilán Azor (*Accipiter gentilis*) están disminuyendo debido a los tratamientos de manejo forestal, los cuales alteran el rango de las condiciones ambientales benéficas para su reproducción y sobrevivencia. Para desarrollar estrategias de conservación efectivas del gavilán, se requiere información de factores intrínsecos y extrínsecos los cuales influencien la buena salud del gavilán. Revisamos la literatura para informarnos de los factores que comúnmente limitan a las poblaciones de aves, y fueron por consiguiente, potencialmente limitantes poblaciones de gavilán. Evaluamos la importancia relativa de estos factores y discutimos cómo y a qué escala estos factores operan para limitar las poblaciones de gavilán. La disponibilidad de alimento y la estructura del bosque parecen ser los factores más omnipresentes que limitan al gavilán, pero el grado en el que dichos factores afectaron a las poblaciones de gavilán. también parece depender de sus interacciones con otros factores, tales como el clima, depredación, competencia y enfermedades, las cuales operan cada una a múltiples escalas espaciales y temporales. Mientras los gavilanes aparecen principalmente en bosques y tierras forestales, el grado en el cual ellos están limitados a la composición y a la estructura del bosque es equívoco, ya que los gavilanes, tanto a nivel individual como a nivel de población, utilizan una amplia variedad de condiciones estructurales mientras forrajean, mucho de lo cual parece estar relacionado a la diversidad de los hábitats ocupados por sus presas. Nuestra revisión sugirió que la disponibilidad de sitios de nidos adecuadamente boscosos, influye fuertemente el sitio de ocupación y de reproducción del gavilán, pero dichas condiciones estructurales del bosque, más allá del sitio del nido, quizás influencien más la reproducción y la sobrevivencia del gavilán, al afectar la abundancia y la accesibilidad de su presa. Esto resalta la importancia de las estrategias de conservación, las cuales dirijan un rango de necesidades del ecosistema, y que integren los requerimientos de la comunidad presa del gavilán, con los componentes estructurales del bosque de los sitios de los nidos del gavilán y los hábitats de forrajeo.

Many questions relevant to wildlife conservation involve factors that limit the distribution and abundance of a species. Such factors include biotic and abiotic features of an organism's environment that affect individual fitness and important population processes. While raptor populations are normally regulated by interactions between resource levels and density-dependent factors, human impacts such as disturbance, pollutants, and resource management may accentuate these factors and lead to reduced viability (Newton 1991). Goshawk populations in both North America (*Accipiter gentilis atricapillus*) and in Eurasia (*A. g. gentilis*) are thought to be declining due to changes in forest conditions caused by management activities, especially tree harvests (Reynolds et al. 1982, Kenward and Widén 1989, Crocker-Bedford 1990, Kennedy 1997, Kennedy 2003). As a result, the status of goshawk populations in North America has been the object of considerable conservation interest (Reynolds et al. 1992, Kennedy 1997, Crocker-Bedford 1998, DeStefano 1998, Kennedy 1998, Smallwood 1998, Andersen et al. 2004) and litigation (Silver et al. 1991, Martin 1998, Peck 2000). Although a variety of factors may contribute to the stability of goshawk populations, a negative cause-effect linkage is often implied between forest management (e.g., loss of old forests) and goshawk viability.

Stability in raptor numbers is often attributed to density-dependent factors, such as food and breeding sites, that affect populations through a negative feedback process between population size and growth rates arising from increased competition for critical resources. Instability in raptor numbers is often attributed to density-independent factors, such as weather and habitat disturbance, that alter the range of environmental conditions required for survival and reproduction (Newton 1991). Disturbance, whether natural or human-induced, can also affect raptor populations by changing the abundance and availability of resources which in turn, may influence other ecological relationships such as competition, predation, or disease. Developing effective conservation strategies requires an understanding of the life history of goshawks as well as the relative importance of factors that limit their populations.

We reviewed the literature for information on factors limiting goshawk populations, and evaluated the evidence for how and at what scale these factors acted on goshawk vital rates. We define a factor as limiting if changes in the factor result in a new probability distribution of population densities due to its affect on survival or reproduction (Williams et al. 2002). Our review focused on factors that commonly limit avian populations, and therefore potentially limit goshawk populations. These factors included food, vegetation composition and structure, predators, competitors, disease, and weather. We view these factors as important components of goshawk habitat, i.e., the collection of biotic and abiotic factors that allow occupancy by goshawks (Hall et al. 1997, Andersen et al. 2004). Our literature review was mostly limited to factors affecting goshawk reproduction and survival. This was because little information exists on goshawk emigration and immigration, two processes that can affect goshawk population dynamics. We did not view this lack of information fatal to our objective because changes in reproduction and survival often have the greatest impact on population dynamics in raptors, and because individuals must be born and survive to emigrate (Noon and Biles 1990, Boyce 1994, Sæther and Bakke 2000). Our review focused on goshawks in North America, but because Eurasian goshawks have similar habitat requirements, hunting techniques, and prey species, we included information on Eurasian goshawk ecology and demographics where pertinent.

POTENTIAL LIMITING FACTORS

Territoriality and Intraspecific Competition

Territoriality is an intrinsic mechanism that reduces intraspecific competition for resources and operates to adjust breeding densities to local resource abundance (Newton 1979a). Territoriality constrains breeding densities by setting an upper limit to the number of breeding individuals that can occupy a habitat patch (Newton 1991). Because territorial interactions occur within the defended part of a home range, territoriality operates to limit goshawks at a scale between the nest area and the home range (Fig. 1). However, the expression of territoriality can affect the numbers of breeding goshawks at spatial scales up to the population level. For example, competition for a limited number of breeding sites can result in a surplus of non-territorial hawks. If a local breeding area is saturated with territorial hawks, individuals without territories are forced into non-breeding status where they must either wait for a breeding vacancy or emigrate. Thus, non-territorial individuals can stabilize goshawk populations by either replacing mortalities on local territories or emigrating to other populations. Where strong competition occurs for territories and non-breeders are abundant, newly recruited individuals are often of an advanced age. Hence, age at first breeding has

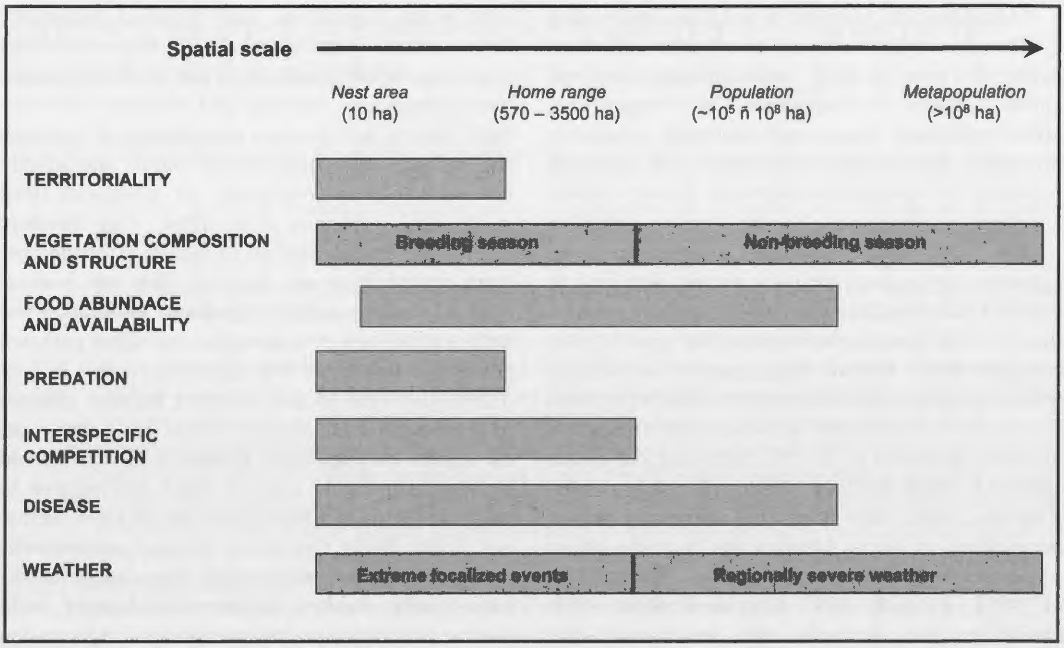

FIGURE 1. Range of spatial scales at which various physical and biotic factors usually operate to limit Northern Goshawk reproduction and survival. Note that the effects of each factor, summed over individuals and pairs of goshawk, can affect their density, reproduction, and survival at the population or even metapopulation levels. Temporal scales at which these factors may operate are not shown.

been proposed as an indicator of population stability (Kenward et al. 1999, Balbontín et al. 2003).

A regular spacing of breeding territories (Reynolds et al. 1994, Woodbridge and Detrich 1994, Reynolds et al. 2005; Reynolds and Joy, *this volume*), stability in territory distribution over time (Reynolds et al. 2005), a surplus of non-breeders (Widén 1985b, Hunt 1997), and a delayed age at first breeding (Wiens and Reynolds 2005) suggest that goshawk breeding density can be limited by territoriality. For example, in Arizona, a high density of regularly spaced goshawk territories (8.6/100 km^2), a temporally constant survival rate of breeding adults (75%), a high territory fidelity rate (94%), and delayed age at first breeding ($\bar{x}$ = 4.2 yr), suggested a high level of competition for a limited number of breeding sites (Reynolds et al. 1994, Reich et al. 2004, Reynolds et al. 2004, Wiens et al. 2006b; Reynolds and Joy, *this volume*). However, while territoriality may set upper limits to the number of breeding goshawks, other factors may determine whether territorial pairs actually breed. Moreover, not all forests are likely to have equal carrying capacities of breeders because the size of goshawk territories within and among landscapes may vary in relation to the demographic structure of populations, variation in local forest conditions, or spatial and temporal variations in resource abundance.

Vegetation Composition and Structure in the Breeding Season

Our review showed that the composition and structure of vegetation used by goshawks during the breeding and non-breeding seasons often differed. Therefore, we reviewed the literature for vegetation effects on goshawk vital rates during the breeding as well as the non-breeding seasons. During breeding, goshawk movements are energetically limited to a finite space around their nest (Krebs et al. 1987); the used space defines the breeding home range. A restricted use of space by breeding goshawk suggests that vegetation composition and structure limits goshawk reproduction and survival at the home range scale (Fig. 1). Estimated sizes of goshawk breeding season home ranges varied from 570–10,823 ha, depending on gender, landscape configuration and availability of forests, and data collection and estimation method (Titus et al. 1994, Squires and Reynolds 1997, Boal et al. 2003).

Goshawks nest in most of the forests and woodlands that occur within their geographic breeding range. The principal forest types occupied by goshawks in North America include coniferous forests, deciduous forests, and mixed coniferous-deciduous forests (Marshall 1957, McGowan 1975, Reynolds et al. 1982, Speiser and Bosakowski 1987, Doyle and Smith 1994, Lang 1994, Reynolds et al. 1994, Woodbridge and Detrich 1994, Beier and Drennan 1997, Squires and Reynolds 1997, Daw and DeStefano 2001). The horizontal and vertical structure of these forests and woodlands vary widely with some types lacking tall trees or continuous canopies (Franklin and Dyrness 1973, Eyre 1980, Barbour and Billings 1988). Tall trees and continuous canopies are characteristics often thought to be necessary for successful goshawk breeding. However, in far northern regions where trees are not available, goshawks have been known to nest on rocks or the ground (Dement'ev et al. 1966, Wattel 1973). Studies of vegetation used by breeding North American goshawks showed that mature and old forests with relatively closed canopies are used most often (Austin 1993, Bright-Smith and Mannan 1994, Hargis et al. 1994, Beier and Drennen1997, Drennen and Beier 2003), but that mid-aged and younger forests (Fischer 1986, Austin 1993, Bright-Smith and Mannan 1994, Hargis et al. 1994), forests adjacent to meadows (Hargis et al. 1994), and open shrub or tundra areas containing scattered patches of trees were also used (Bent 1938, White et al. 1965, Swem and Adams 1992, Younk and Bechard 1994a). Nonetheless, annually consistent higher breeding densities in tall, canopied forests suggest that contiguous forests composed of tall trees provide better habitat for goshawks (Reynolds and Meslow 1984, DeStefano et al. 1994a, Woodbridge and Detrich 1994, Reynolds et al. 1994; Reynolds and Joy, *this volume*; but see Younk and Bechard 1994a, b).

Goshawks typically place their nests in forest patches comprised of large trees. Because nest areas are a small fraction of the home range, they typically have a lower diversity of vegetation types and seral stages then the remainder of the home range, much of which used for hunting (Reynolds et al. 1992, Hargis et al. 1994, McGrath et al. 2003). We therefore partitioned our assessment of breeding season vegetation as a goshawk limiting factor into the nest and foraging areas (Reynolds et al. 1992). These two areas are consistent with the spatial scales used in most investigations of goshawk habitat (Andersen et al. 2004).

Nest Area

Availability of nest sites often limits bird populations as shown by increases in their populations after the placement of artificial nests in areas that otherwise appeared suitable (Cavé 1968, Reese 1970, Rhodes 1972, Hammerstrom and Hammerstrom 1973, Newton and Marquiss 1983, Village 1983, Newton 1991). Goshawk nest habitat has been variously partitioned into the nest site, habitat immediately surrounding the nest (Reynolds et al. 1982, Squires and Reynolds 1997), the nest area, a 8–10 ha area surrounding a nest that includes the hawk's roosts and prey plucking sites (Newton 1979a, Reynolds et al. 1992), and the nest stand, and the stand of trees homogenous in vegetation composition and structure that contains a nest (Reynolds et al. 1982, Woodbridge and Detrich 1994). The size of nest stands can be highly variable and their frequency of use by breeding goshawks has been shown to increase with nest stand size. In California, where nest-stand boundaries were defined by edges of forest-management treatments, lava flows, and meadows, nests in small forest stands (<20 ha) were only occasionally occupied, whereas nests in larger stands (>60 ha; maximum = 115 ha) were occupied more often (Woodbridge and Detrich 1994). However, while we believe that it is likely that a minimum forest patch size for sustaining goshawk nesting exists, we question whether the relationship identified by Woodbridge and Detrich (1994) might simply reflect the fact that most alternate nests of goshawks tend to be near the center of their territories (Reynolds et al. 2005; Reynolds and Joy, *this volume*) and that, as stand size increases, the alternate nests are included within the stand. Because of the large reported variability in sizes of nest stands and because a nest site does not encompass a pair's roosts and prey handling areas, we believe that the nest area is the best scale at which to describe goshawk nest habitat.

While the variety of forest types occupied by goshawks is suggestive of their adaptability to diverse forest compositions, goshawks demonstrate considerable specificity in choice of vegetation structure in nest areas. Nest area vegetation structure consistently includes a relatively high density of mature or old trees, high canopy cover, and an open understory (Squires and Reynolds 1997). High tree density and canopy closure within a nest area has been associated with increased territory occupancy and nesting rates (Keane 1999, Finn et al. 2002b). Because of the consistency of these nest area vegetation structures, and because tree species composition is so highly variable, structure appears to be more important than species composition in goshawk choice of nest areas (Erickson 1987, Reynolds et al. 1992, Rissler 1995).

Uniformity in vegetation structure among goshawk nest areas is also evident in comparisons of nest area vegetation to vegetation within the home range. Hargis et al. (1994), Daw 1997) and McGrath et al. (2003) found that the diversity of vegetation characteristics (e.g., forest age classes, canopy closures, basal areas, and openings) surrounding goshawk nests increased with distance from nests. Not surprisingly, difference between nest area and home range vegetation is greatest where goshawks nest in small stands of trees in non-forested landscapes (Bond 1940, White et al. 1965, Dement'ev et al. 1966, Swem and Adams 1992; Younk and Bechard 1994a, b).

While nest areas with large trees and dense canopies appear to be preferred by goshawks, the extent to which they are required for successful nesting is uncertain because goshawks tolerate some reduction in these structural conditions. For example, Penteriani and Faivre (2001) and Penteriani et al. (2002b) reported continued use of nest areas by European goshawks when up to 30% of trees within 50 m of the nest tree were lost by windstorm damage or logging. Nonetheless, identifying the effects of nest area disturbance on goshawk occupancy can be confounded by: (1) individual goshawk variability in among-year fidelity to a nest (R. Reynolds, unpubl data), (2) the difficulty of determining whether the lack of suitable alternate nests constrained goshawk movement among nests, and (3) a potentially high natural (irrespective of disturbance) frequency of movement among alternate nests (55–76% of egg-laying goshawks annually moved to alternate nests in Arizona; Reynolds et al. 2005; Reynolds and Joy, *this volume*).

Foraging Area

Foraging habitat is where goshawks search, pursue, and capture prey. Our review showed that relatively little is known about how and which vegetation types and seral stages outside of nest areas are used by hunting goshawks (Schnell 1958). This limited understanding stems from the difficulty of observing goshawks due to their elusive behavior, the density of the forest vegetation they occupy, and their rapid movements through large home ranges resulting from their short-perch-short-flight hunting behavior (Kenward 1982, Widén 1985b). Because of these difficulties, most observations of goshawk behavior and movements comes from radio-telemetry studies. Nonetheless, the usefulness of radio telemetry for understanding goshawk behavior can be limited. First, numbers of goshawks included in most radio-telemetry studies were small, thereby limiting inferences to populations. Second, the limited range over which a transmitter's signal can be received (especially in forests and mountainous terrain) can result in a hawk being out of range during periods of a study, potentially biasing estimates of home range size, behavior, and vegetation use. Third, the elusiveness of goshawks often makes it necessary to triangulate using ≥2 observers or use radio signal strength to estimate a goshawk's location, potentially resulting in large location errors (Bright-Smith and Mannan 1994, Titus et al. 1994, Boal et al. 2003). Finally, because radio-tagged goshawks are seldom observed directly, their behavior is usually unknown (Bright-Smith and Mannan 1994). In spite of these shortcomings, radio telemetry remains the best tool to study the behavior and habitat use by goshawks.

As the number of telemetry studies increases, it is increasingly evident that within and among the geographically varied regions and forest types occupied by goshawks, the diversity of vegetation structural and seral stages used by individuals is strikingly broad. Vegetation types used by individuals ranged from young to old forests, from early seral to late-seral forests, from closed-canopied to open forests, woodlands, and shrub-steppe with highly fragmented tree patches, and from forest interiors to edges and openings. Nonetheless, when individual goshawks were pooled within studies (excluding studies in which goshawks hunted in shrub-steppe), typically a preference was observed for mature and old forests (Kenward 1982, Widén 1985b, Austin 1993, Bright-Smith and Mannan 1994, Hargis et al. 1994, Titus et al. 1996, Younk 1996, Beier and Drennan 1997, Good 1998, Lapinski 2000, Boal et al. 2000, Bloxton 2002, Stephens 2001, Drennan and Beier 2003). Goshawk use of such a broad diversity of vegetation structures shows a level of behavioral adaptability that suggests that if nest sites and foods were not limiting, goshawks could breed in most if not all forests and woodlands within their range. Where goshawks occur in more canopied forests their selection for mature and old forest age appears to be in accordance with the vegetation structure best suited to their morphology and hunting behavior and where many of their prey are more abundant (Reynolds et al. *this volume*).

A number of non-telemetry studies compared vegetation in plots of increasing radii from nests to determine if goshawks preferentially nested in landscapes with vegetation conditions different from those around random points, and whether different home range vegetation conditions affected goshawk breeding performance. Allison (1996), Daw and DeStefano (2001), Joy (2002), and McGrath et al. (2003) found that differences in vegetation in goshawk nest plots and random plots were greatest in plots with short radii (≤250 m), but the differences diminished with increasing distance from plot centers. These studies demonstrated the importance of older forests in goshawk nest areas, but that beyond nest areas forest composition and structure began to resemble random landscapes. Hall (1984), Joy (2002), and McGrath et al. (2003) found that landscapes surrounding goshawk nests had greater diversity and intermixture of different forest age-classes and vegetation types than landscapes around random points. In contrast, Finn et al. (2002a) reported that historical goshawk nest sites containing a higher proportion of late-seral forests in surrounding landscapes were occupied more often by breeding goshawks than historical nest sites with a lower proportion of late-seral forests in surrounding landscapes.

While these landscape studies implicitly or explicitly tested the hypothesis that mature and old forests are important to goshawk occupancy and reproduction, none determined whether or how goshawks actually used any of the vegetation types or seral stages within plots. While telemetry studies showed that goshawks preferentially used mature and old forests, many showed goshawks using young forests, edges and openings (Bright-Smith and Mannan 1994, Hargis et al. 1994, Good 1998). Use of vegetation types are also likely to shift seasonally and yearly due to changes in seasonal or annual food abundance among the types. As well, temporally changing parental requirements at nests may cause adults to expand their foraging areas (Hargis et al. 1994), which could change the availabilities, and therefore use, of vegetation types. Thus, non-telemetry landscape studies add little to our understanding of how, when, and why goshawks use habitat. A further potential limitation of studies of the relationship between landscape vegetation conditions and frequency of goshawk breeding (Finn et al. 2000) is that they require some level of confidence that the territories are or are not occupied by breeding goshawks. High confidence is difficult to attain, however, because goshawks do not lay eggs every year, and when they do, they more often than not move to an alternate nest. Correctly classifying territories as having breeders can be achieved only by conducting extensive searches for active nests over large areas and several years (Reynolds et al. 2005; Reynolds and Joy, *this volume*).

Much of the diversity of vegetation types and seral stages used by goshawks appears to stem from their entry into the diverse habitats of their prey. In Sweden and Norway, goshawks in boreal forests hunted in mature forests, the habitat of their main prey (tree squirrels; Widén 1989, Tornberg and Colpaert 2001). In farmland and forest mosaics in Sweden, goshawks favored forest edge, the habitat of their main prey there (rabbits and pheasants; Kenward 1977). In both areas, prey abundance was greater in the habitats used by goshawks. In Nevada, goshawks hunted in open shrub-steppe vegetation where their main prey, Belding's ground squirrel (*Spermophilis beldingi*), was abundant in openings (Younk and Bechard 1994a). Belding's ground squirrels were also important in Oregon (Reynolds and Meslow 1984, Daw and DeStefano 1994) where the goshawks likely entered meadows to hunt them. Another important prey in western North America is the golden-mantled ground squirrel (*Spermophilis lateralis*; Reynolds and Meslow 1984, Boal and Mannan 1994, Reynolds et al. 1994, Woodbridge and Detrich 1994). This ground squirrel occurs in open forests, meadows, and associated edges, where they were presumably hunted by goshawks. In Sweden, wintering goshawk habitat use (preferred mature forests, avoided younger forests and used agricultural lands, wetlands, and clearcuts proportional to the availability) was associated with higher prey density and vegetation features that influenced a goshawk's ability to successfully hunt (Widén 1989).

Evidence contrary to the supposition that goshawks select foraging habitat based on prey abundance comes from sites where radio-tagged goshawks were assumed but not directly observed to have been foraging, where they presumably killed prey based on changes in transmitter pulse rates, where goshawks were observed feeding, and where the remains of their prey were found. Beier and Drennan (1997) investigated the relative importance of vegetation structure versus prey abundance on goshawk choice of foraging habitat by comparing vegetation attributes and indices of prey abundance at locations where radio-tagged goshawks were assumed to have hunted to vegetation and prey abundance at randomly located plots. They argued that forest structure was more important than prey abundance because goshawk hunting plots had more large trees with higher canopy closure than random plots and there was no significant differences in prey indices at foraging sites and random plots (Beier and Drennan 1997). Good (1998) also characterized forest structure and relative prey abundance at sites where radio-tagged goshawks killed prey. He suggested that, on average, forest structure had a greater influence on the repeated use of kill sites than prey abundance because goshawks returned more often to kill sites with greater densities of large trees and less shrub cover than to kill sites with higher prey abundances (Good 1998). We believe, however, that inferences about a goshawk's choice of hunting habitat based on foraging or kill sites are equivocal for several reasons. First, we find that judging whether or not goshawks were hunting based on telemetry signals, or even when directly observed, to be problematic. Second, we question the validity of the assumption that kill sites (as judged by prey remains or observations of feeding goshawks) are necessarily the same sites where the prey was first detected by goshawks. This assumption requires that the bird and mammal prey did not attempt to escape and thereby leave the detection site before being captured. Furthermore, goshawks often move their prey to denser hiding cover while feeding, and, during the breeding season when they deliver food to nests, they sometimes stop to pluck their prey on the way (R. Reynolds, pers. obs.). Misidentifying plucking or feeding sites as kill sites in these situations could introduce a systematic bias towards denser vegetation. Finally, studies using indices of prey abundance fail to account for variation in bird and mammal detection probabilities due to among-plot differences in vegetation structure. Failure to account for variable detection probabilities can lead to unreliable estimates of animal abundance (Buckland et al. 2001).

Reynolds et al. (1992) developed management recommendations for forests in the southwestern US by combining existing information on (1) the structural components of goshawk nest areas with (2) vegetation structures thought suited for goshawk foraging given their morphology and behavior with (3) the structural and seral stages of vegetation that provides the habitats of the community of goshawk prey species (Reynolds et al., *this volume*). Short wings, long tail, and a short-perch, short-flight hunting tactic (Kenward 1982, Widén 1985a) are morphological and behavioral adaptations of goshawks for hunting in forests where prey searching fields are obscured by tall and dense vegetation. Because many prey species occur in the lower vegetation column, goshawk prey searching is focused toward the ground and lower forest layers (Reynolds and Meslow 1984). The size of the search field around a hunting perch depends on the height and density of surrounding trees, density and composition of understory vegetation, prey location, and goshawk perch height (Janes 1985a, b). Presumably, goshawks change their perching time, height, and location in accordance with these structural characteristics to increase encounters with prey (Schipper et al. 1975, Baker and Brooks 1981, Bechard 1982). In the Southwest, older forest with tall trees and lifted crowns were recommended because goshawks need flight space below the forest canopy and open understories enhance the detection and capture of prey (Reynolds et al. 1992). The idealized home range also contained a diversity of vegetation types and seral stages, including small openings, to provide the habitats of the goshawk's diverse suite of prey (Reynolds et al. 1992).

Vegetation Composition and Structure in the Non-breeding Season

Goshawks are typically year-round residents, especially during winters when prey is abundant (Speiser and Bosakowski 1991, Doyle and Smith 1994, Boal et al. 2003). However, some adult goshawks regularly winter outside of their breeding areas (Squires and Ruggiero 1995, Squires and Reynolds 1997). Squires and Reynolds (1997) reported that adult goshawks in Wyoming wintered as far as 346 km from their nests, and Wiens et al. (2006b) reported that the majority of juvenile goshawks left their conifer forest habitat for low elevation woodlands and shrub-steppe shortly after dispersing from their natal area, and that some of these made movements as far as 442 km in their first fall. Estimates of home-range size for goshawks that stay on or close to their breeding home range during the non-breeding season (October–February) are typically much more variable (1,000–8,000 ha) than breeding home ranges (Boal et al. 2003; Sonsthagen et al., *this volume*; Underwood et al., *this volume*). Winter expansion of space use suggests that the vegetation component of goshawk habitat during the non-breeding season may operate to affect goshawk survival at larger spatial scales then during breeding (Fig. 1). In North America, the vegetation component of goshawk winter habitats has been studied far less than their breeding habitats, making it difficult to assess the importance of vegetation as a factor limiting goshawks during the non-breeding season. Wiens et al. (2006b) reported increased mortality of radio-marked juvenile goshawks following dispersal from their natal territories and movement into pinyon-juniper woodlands and shrub-steppe. Squires and Ruggiero (1995) reported predation by eagles on adult goshawks that had also moved into shrub-steppe. These studies suggest that movements to vegetation types that provide little cover increases mortality.

particularly of inexperienced juveniles (Squires and Ruggiero 1995, Wiens 2004).

The composition and structure of vegetation used by wintering goshawks varies within and among regions and probably depends to some extent on the degree of landscape heterogeneity in the vicinity of breeding habitat. In western North America where montane forest habitats are surrounded by lower elevation woodland, shrub-steppe, and desert, winter home ranges include a higher diversity of vegetation types then breeding areas (Squires and Ruggiero 1995, Stephens 2001). While it is unknown why some adult goshawks move from forests to open woodlands, shrublands, desert scrub, and agricultural areas during the non-breeding season, some of this movement could be in response to extreme weather or low winter prey abundance in montane forest habitat (Doyle and Smith 1994, Reynolds et al. 1994, Squires and Ruggiero 1995, Stephens 2001, Drennan and Beier 2003; Underwood et al., *this volume*). Radio-telemetry studies show that adult goshawks often stayed on their breeding areas in winter (Reynolds et al. 1994, Doyle and Smith 1994, Boal et al. 2003).

Studies in Europe suggest that food may be a more important limiting factor than vegetation structure during the non-breeding season (Widén 1989, Kenward et al. 1999, Sunde 2002). Contrarily, some evidence shows that wintering goshawks selected habitat based on structure rather than prey abundance. Drennan and Beier (2003), studying radio-tagged goshawks in Arizona, found that canopy closure and density of medium-sized trees (20–40 cm dbh) were higher at foraging sites than randomly-located sites and there were no difference in indices of prey abundance at kill and random sites. These authors hypothesized that goshawks probably do respond to prey abundance when locating a home range, but that they select older forest conditions within the home range where they can best use their maneuverability to capture prey (Drennan and Beier 2003). Stephens (2001) investigated whether vegetation characteristics at winter kill sites of radio-tagged goshawks in Utah differed from random locations. Differences were detected only in tree diameter and canopy closure, which were higher at kill sites. Potential problems with using foraging sites for determining non-breeding foraging habitat use are similar to those discussed above.

Food Availability

Food availability is a function of both food abundance and a consumer's access to the food. Goshawks typically eat a variety of prey species including ground and tree squirrels, rabbits and hares, medium to large passerines, woodpeckers, and grouse (Squires and Reynolds 1997; Reynolds et al., *this volume*). The diet of a local goshawk population depends in part on the composition of the local bird and mammal fauna which typically varies among vegetation types. Prey availability can vary seasonally and annually according to the extent to which their populations undergo annual fluctuations or seasonal changes in abundance due to the timing of their reproduction, migration, aestivation, or hibernation. In addition to a vegetation influence on prey availability, differences in size, color, age, and behavior also influence prey's availability to goshawks. Thus, based on goshawk foraging behavior, differences in suites of prey among vegetation types, and effects of local and region-wide weather patterns on prey populations, we believe that food availability limits goshawks at the home range to metapopulation scales (Fig. 1).

Food supply affects the distribution and abundance of raptors, the sizes of their territories or home ranges, the proportion of pairs breeding, nest success, and number of young produced (Schoener 1968; Southern 1970; Galushin 1974; Baker and Brooks 1981; Salafsky 2004, 2005). In goshawks, many of these demographic parameters vary considerably among years (Squires and Reynolds 1997, McClaren et al. 2002, Reynolds et al. 2005; Keane et al., *this volume*). Several studies of goshawks in North America and Europe identified a close association between annual fluctuations in goshawk reproduction (proportion of pairs breeding, timing of egg laying, clutch size, and fledgling production) and annual fluctuations in prey abundance (McGowan 1975: Sollien 1979; Lindén and Wikman 1980; Huhtala and Sulkava 1981; Doyle and Smith 1994; Keane 1999; Salafsky 2004, 2005). However, in Germany, prey abundance was not a major limit to goshawk population growth rate, presumably because the local prey base was diverse (>60 prey species) and prey populations remained relatively stable over time (Krüger and Lindström 2001). Because female raptors must accumulate body fat and protein reserves to produce eggs, low prey abundance early in the breeding season may result in a failure to lay eggs, delayed egg laying, smaller clutches, or nest failures (Newton 1979a, 1991). This also appears to be the case in goshawks, as indicated by close associations between goshawk reproduction and the relative abundance (Keane et al., *this volume*) and density (Salafsky et al. 2005) of prey in the spring.

Density, physiological condition, and survival of goshawk fledglings, juveniles, and adults also appear to be directly related to food availability. Decreases in goshawk numbers were attributed to the rarity of rabbits in Spain (Cramp and Simmons 1980), and goshawks wintering in Sweden were more abundant and had greater body mass in areas with higher pheasant availability (Kenward et al. 1981b). In Norway, likelihood of starvation in goshawks, particularly juvenile males, increased with latitudinal gradient in the northernmost range of the species, perhaps due to a gradient in prey availability or biomass (Sunde 2002). Large annual differences in the density of primary bird and mammal prey species on the Kaibab Plateau, Arizona explained 86% of annual variation in juvenile survival through the first 3.5 mo post-fledging, and starvation was identified as the leading cause of mortality in years when prey was relatively scarce (Wiens et al. 2006a). In New Mexico and Utah, supplemental feeding experiments showed that surplus food during the nestling and fledgling-dependency periods increased fledging success, and that food appeared to interact with parental care and sibling competition to regulate post-fledgling survival (Ward and Kennedy 1996, Dewey and Kennedy 2001). The many instances of food limitation in the literature suggested to us that food is a important and ubiquitous factor limiting goshawk reproduction and survival.

Predation

Goshawk reproduction and survival rates may depend on the abundance of predators and the frequency of exposure to them. Predators of goshawks include Great Horned Owls (*Bubo virginianus*; Rohner and Doyle 1992), eagles (Squires and Ruggiero 1995), Red-tailed Hawks (*Buteo jamaicensis*; Wiens 2004), and mammals such as martens (*Martes americana*; Doyle 1995) and wolverines (*Gulo gulo*; Paragi and Wholecheese 1994,), and perhaps foxes (*Vulpes, urocyon*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and raccoons.(*Procyon lotor*). Of these, Great Horned Owls may be the most important because of their killing capacity and their abundance in the North American range of goshawks (Orians and Kuhlman 1956, Luttich et al. 1970, McInvaille and Keith 1974, Houston 1975). For goshawks, exposure to predation can be high because goshawks and several species of large forest owls often nest in close proximity (Rohner and Doyle 1992, but see Gilmer et al. 1983). Because other large raptors occupy more open habitats, some authors suggested that tree-cutting may not only increase the numbers of goshawk predators but increase goshawk predation risk by diminishing hiding cover (Crocker-Bedford 1990, La Sorte et al. 2004).

Young goshawks are more susceptible to predation than adults due to their inexperience and poor flight skills. Indeed, most reports of predation are on nestlings, fledglings, and juvenile goshawks. Nonetheless, Great Horned Owls occasionally kill adult goshawks (Rohner and Doyle 1992) but the extent of such losses is unclear. Squires and Ruggiero (1995) reported a likely case of raptor predation on an adult male goshawk that had migrated to open sagebrush during winter. Survival of adult goshawks on the Kaibab Plateau in northern Arizona, an area with abundant Great Horned Owls (R. Reynolds, pers.obs.), was 75% for both females and males (Reynolds et al. 2004). In view of combined but unknown losses to other mortality sources (e.g., age, starvation, accident, and disease), it seems unlikely that predation was a significant mortality factor of adult goshawks on the Kaibab Plateau. Newton (1986) found that predation on Eurasian Sparrowhawks (*Accipiter nisus*), a smaller species with potentially more predators, was of little direct consequence to its population dynamics. Reports of predation on goshawks are typically incidental, and we found no studies that specifically addressed the effects of predation on goshawk vital rates. Because predation appears to occur primarily at or in the vicinity of, nests where whole families of goshawks are susceptible to predation, the scale at which predation is most likely to operate to limit goshawk populations is the nest area (Fig. 1). However, predation can also act at much broader spatial scales by affecting adult survival in wintering areas and the number of dispersing juveniles. An example of this was a doubling of the risk of predation for radio-marked juveniles after they dispersed from natal areas in Arizona (Wiens et al. 2006a).

Inter-Specific Competition

Inter-specific competition is the use of a resource by two or more species such that the combined use limits individual fitness or population size of the competing species (Birch 1957, Emlen 1973). A necessary condition of competition is that a resource must be short of the demand for it. Without knowing if resources are in short supply, or whether competitors are consuming resources from the same area, we can only assume that species with similar geographic ranges, habitats, and diets are potential competitors (Wiens 1989). Different habitat and food preferences among raptor species has been widely noted and often attributed to competition (Janes 1985a, b). Competition among goshawks and other species is likely to be strongest for nest sites and food. Thus, inter-specific competition operates primarily at the nest-site and home-range scales, but it can affect goshawk fecundity and survival at all spatial scales (Fig. 1).

The extent to which goshawk behavior, reproduction, and survival are affected by inter-specific competition is unknown. Goshawks and other raptors often nest in close proximity (Reynolds and Meslow 1984), and Great Horned Owls, Spotted Owls (*Strix occidentalis*), and Great Gray Owls (*Strix nebulosa*) often lay eggs in goshawks nests (Forsman et al. 1984). However, goshawks displaced from nests by owls may simply move to an alternate nest within their territory, so long as alternate nest areas are available. It is unlikely that breeding goshawks could be completely excluded from a forest area by other raptors because territoriality in these other raptors results in wide dispersions of their nests (McInvaille and Keith 1974). Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*Accipiter cooperii*) are potential competitors with goshawks for nest sites and food because their ranges overlap and they occupy similar habitats. However, these smaller hawks are not likely to be strong competitors with goshawks for nests sites because they not likely to be able to exclude goshawks (Reynolds et al. 1982, Moore and Henny 1983, Siders and Kennedy 1994). Red-tailed Hawks are another species sympatric with goshawks that nest in similar forests. However, Red-tailed Hawks more often nest adjacent to forest openings, high on ridges, and in relatively open sites (La Sorte et al. 2004, Titus and Mosher 1981, Speiser and Bosakowski 1988), whereas goshawks typically nest on slopes or in drainage bottoms in relatively denser forest sites (Reynolds et al. 1982, LaSorte et al. 2004). Competition between these species is likely to be low except in naturally open forests or forests fragmented by meadows, burns, or clear-cuts (La Sorte et al. 2004).

Several species of hawks and owls potentially compete for food with goshawks. Cooper's Hawks nest and hunt in the same vegetation conditions and feed on some of the same prey as goshawks (Storer 1966, Reynolds and Meslow 1984). Red-tailed Hawks and Great Horned Owls have significant diet overlap with goshawks, but neither typically eats as many birds as goshawks (Fitch et al. 1946, Smith and Murphy 1973, Janes 1984, Bosakowski and Smith 1992). In Arizona, 48% of Red-tailed Hawk diets consisted of species that occurred in goshawk diets (Gatto et al. 2005). Because Red-tailed Hawks are typically more abundant in open habitats (Howell et al. 1978, Speiser and Bosakowski 1988), the extent to which they compete for food probably varies by the openness of forest type or the extent of forest fragmentation. In most North American forests, a variety of mammalian carnivores including foxes, coyotes, bobcats, lynx (*Lynx canadensis*), weasels (*Mustela* spp.), and martens co-occur in forests with goshawks and feed on many of the same prey species. While the combined effects of food depletion by these competitors on the abundance and distribution of goshawks is unknown, competition for food among these species may be high when prey populations are low. For example, numerous co-occurring species of mammalian carnivores, owls, and hawks in Sweden consumed large numbers of small vertebrate prey, and their combined consumption resulted in food limitations for several of them (Erlinge et al. 1982).

Disease and Parasitism

Although many diseases and parasites have been reported in raptors, information on the distribution of disease organisms, and on individual and species-specific raptor differences in susceptibility to infections is limited. Because few studies have addressed diseases in wild goshawks, much of our evaluation of disease as a goshawk limiting factor was inferred from the incidence and effects of disease in other raptors. Some common raptor diseases are erysipelas, salmonellosis, botulism, aspergillosis, avian leucosis, Newcastle disease, bronchitis, laryngotracheitis, pox, herpesvirus hepatitus, miliaria, coccidia, trichonomonas, a variety of intestinal round worms (*Capillaria* and *Serratospiculun*), myiasis, and mallophaga (Newton 1979a). The distribution and abundance of these disease organisms vary by season, habitat, and region. Susceptibility to disease is dependent on raptor behavior, diet, body condition, age, genetic predisposition, and chance (Alverson and Noblet 1977, Schröder 1981, Newton 1986, Phalen et al. 1995, Newton 1991). Schröder (1981) reported that 68 of 105 eagles and hawks had infectious and parasitic diseases compared to 19 of 45 falcons. Schröder (1981) and Delannoy and Cruz (1991) found that 14% of captive eagles and hawks died from tuberculosis and 21% were affected with mycoses, suggesting that among raptor diseases caused by pathogens, bacterial infections are of the greatest importance. Disease and parasites have been associated with abnormal behavior, nest desertions, and reduced mating success, clutch sizes, hatching success, and nestling growth and survival of juveniles (Newton 1991). For example, female Boreal Owls (*Aegolius funereus*) with higher levels of blood parasites had smaller clutch sizes than females with fewer blood parasites (Korpimäki et al. 1993). Infestations of the warble fly (*Philornis* spp.) on Puerto Rican Sharp-shinned Hawk nestlings accounted for 69% of nest failures (Delannoy and Cruz 1991), and trichomoniasis killed 22% of Cooper's Hawk nestlings in the urban area where the hawks fed on doves, a presumed carrier of the protozoan *Trichomonas gallinas* (Boal and Mannan 1999, 2000).

Among *Accipiter*, Newton (1986) found disease practically non-existent in a population of Eurasian Sparrowhawks he studied for 14 yr in Scotland. However, five of 10 goshawks had blood parasites in Britain (Peirce and Cooper 1977) and 22 of 31 goshawks had parasites in Alaska (McGowan 1975). Redig et al. (1980) reported aspergillosus (*Aspergillus fumigatus*) in 26 of 49 (53%) and three of 45 (7%) wild goshawks trapped in Minnesota in 1972 and 1973, respectively. In New Mexico, Ward and Kennedy (1996) reported that one of 12 juvenile goshawks died of disease, as determined by necropsy. Cooper and Petty (1988) found an approximate 15% reduction in goshawk productivity due to nestling deaths from blood parasites. However, in many birds, parasitism is responsible for fewer nestling deaths than predation (Newton 1991).

A number of new epizootics may threaten raptor populations, one of which is West Nile virus (WNV; Daszak et al. 2000). Factors such as the distribution and population size of susceptible hosts, the size and distribution of vector populations, and the presence of suitable habitat characteristics all contribute to the transmission of WNV (Deubel et al. 2001, Petersen and Roehrig 2001). Anecdotal evidence indicates that captive goshawks suffer high mortality when exposed to WNV (J. Scherpelz, Rocky Mountain Raptor Program, pers. comm.), but some raptors appear capable of developing resistance to WNV; mortality of rehabilitated and wild owls declined during their second year of exposure WNV (Caffrey and Peterson 2003). Although the effect of WNV on wild goshawks is uncertain, we suspect that a concern will continue because of its known effect on many bird species. While disease appears most commonly to effect goshawks at the individual level (home-range scale), disease may affect goshawk fecundity and survival at the population scale. The spread of disease beyond the population scale is likely to be restricted by the distances between metapopulations (Fig. 1).

The importance of disease as a goshawk limiting factor is unknown because disease often predispose individual raptors to other mortality agents (Esch 1975), and food shortages may predispose goshawks to disease. Hence, it is not often clear whether mortality due to disease is additive or compensatory (Robinson and Holmes 1982). However, when compared to starvation and trauma, disease was not a significant cause of mortality in eagle and hawk populations studied by Keymer et al. (1981) and Redrobe (1997). On the Baltic island of Gotland, only 3% of goshawk deaths were caused by disease as compared to 15% from starvation and 10% from trauma (Kenward et al. 1993a). Although disease has been identified in captive and wild goshawks, no strong evidence indicates that disease is a significant factor limiting their populations (USDI Fish and Wildlife Service 1998a, Kennedy 2003).

WEATHER

Weather can affect bird populations in two ways: within-year effects, reflecting sudden, extreme, and episodic events; and among-year effects, reflecting weather variation over larger temporal and spatial scales (Rotenberry and Wiens 1991). Extreme weather events such as hail storms and wind storms can cause direct mortality of eggs, nestlings, juveniles and adults, or indirect mortality by damaging vegetation structure and food supplies. Prolonged periods of regionally severe weather such as droughts or winters with heavy snow may have strong indirect effects on goshawk reproduction and survival by reducing food availability. Weather can act as a goshawk limiting factor at multiple spatial scales, from a single individual or nest by a localized event, e.g., hail, wind, to populations and metapopulations during region-wide severe weather such as drought (Fig. 1).

Inter-annual variation in raptor reproduction has been closely tied to variation in local weather conditions (Franklin et al. 2000, Dreitz et al. 2001, Krüger and Lindström 2001, Bloxton 2002, Seamans et al. 2002). Snowy winters can reduce prey availability during courtship, a period when females need energy for egg laying, leading to lowered numbers of breeding goshawks (Kostrzewa and Kostrezewa 1990). Cold and wet springs can lead to delayed egg laying, and prolonged rain periods can affect brood sizes, presumably by reducing the hunting activity of adults and by lowering prey availability (Newton 1986, Kostrzewa and Kostrzewa 1990, Patla 1997, Penteriani 1997). Several goshawk studies showed that heavy spring precipitation lowered nesting success and that mild spring temperatures favored increased goshawk reproduction (Kostrzewa and Kostrzewa 1990, Patla 1997, Penteriani 1997, Krüger and Lindström 2001; Keane et al., *this volume*), but see Ingraldi (1998) for a positive relationship between spring precipitation and productivity). Kostrezewa and Kostrzewa (1990) found that variations in spring rainfall and temperature affected breeding success in goshawks more than any other factor, and Krüger and Lindström (2001) found that increased precipitation during the nestling phase and autumn periods had a strong negative effect on goshawk population growth rate. Demographic studies of Spotted Owls found that nearly all of the temporal process variation in reproductive output was explained by weather (Franklin et al. 2000, Seamans et al. 2002, LaHaye et al. 2004), and we predict that a large proportion of temporal process variation in goshawk reproduction also will be explained by weather.

Goshawk nestlings are poor at regulating their body temperature in the first 10–15 d after hatching, making them more vulnerable to weather extremes than juveniles or adults. However, even late-term nestlings are susceptible. In Arizona, for example, increased mortality of late-term nestlings was observed during 10-d of continuous rain in 1998 (R. Reynolds, pers. obs.). However, in the same study population and in the same year, Wiens et al. (2006a) found no indication that continuous, heavy rainfall affected the survival of radio-tagged juvenile goshawks once they had fledged. Sunde (2002) also found no effects of temperature or precipitation on relative starvation risk or body condition of juvenile or adult goshawks recovered dead in Norway.

SYNTHESIS AND CONCLUSIONS

We reviewed information on the biology of goshawks relative to several well-known avian population limiting factors including food, vegetation compositions and structure, predation, competition, disease, and weather. While we found numerous sources of information on how some of these factors limited goshawk reproduction, many uncertainties remain regarding how these factors affect survival, particularly of adults. Adding to this uncertainty is the inadequacy of demographic data on goshawks to properly assess population trends irrespective of limiting factors (Andersen et al. 2004; Squires and Kennedy, *this volume*). This inadequacy precluded a quantitative evaluation of how these limiting factors influence goshawk population dynamics. The great variability in habitats occupied by goshawks combined with methodological differences among studies in data collection and analyses restricted our assessment of the relative importance of the different limiting factors as well. Nevertheless, several important patterns emerged from our review.

A number of studies identified a tie between vegetation characteristics around goshawk nests and territory occupancy and reproduction (Crocker-Bedford 1990, Woodbridge and Detrich 1994, Keane 1999; Finn et al. 2002a, b; Joy 2002, Penteriani et al. 2002a). However, no study to our knowledge quantified a direct relationship between goshawk survival and vegetation composition and structure, either in breeding habitats or in winter habitats, although some evidence suggests that predation on goshawks may be higher in non-forested habitats. Several studies established an association between food abundance and goshawk reproduction (McGowan 1975; Sollien 1979; Lindén and Wikman 1980; Huhtala and Sulkava 1981; Doyle and Smith 1994; Keane 1999; Salafsky 2004, 2005), and survival (Kenward et al. 1981b, Ward and Kennedy 1996, Dewey and Kennedy 2001, Wiens et al. 2006a). Nearly all long-term goshawk studies reported predation of nestlings and a few reported predation on adults, but none provided evidence suggesting that predation was a primary factor limiting goshawk populations. Little direct information is available regarding the effect of inter-specific competition on goshawks, but at least two studies suggested that competition might have an increasingly negatively affect on goshawks with increasing forest fragmentation and loss of mature forest structure (La Sorte et al. 2004; Gatto et al. 2005). No study found disease to be a major threat to goshawk populations, although there is concern over the arrival of WNV in the goshawk's North American range. In contrast, several studies indicate that goshawk reproduction was influenced by weather (Kostrzewa and Kostrzewa 1990, Patla 1997, Penteriani 1997, Ingraldi 1998, Krüger and Lindström 2001; Keane et al., *this volume*), but evidence of weather effects on goshawk survival were mainly anecdotal, and studies of the direct effects of weather on juvenile and adult survival failed to detect an effect (Sunde 2002, Wiens et al. 2006a).

While lack of evidence is not proof that any of these factors did not significantly affect goshawk populations, considerable evidence suggested that vegetation structure at nest sites and foraging sites, and the abundance and availability of food were the primary factors limiting goshawk reproduction and survival. This is in agreement with Widén (1989), who argued that, based on higher goshawk breeding densities in areas richer in prey, and extremely high goshawk breeding densities in areas with only 12–15% woodland but extremely rich in prey, goshawks were limited more often by food availability than by nesting habitat. The evidence was not clear, however, whether food, nest sites, or vegetation structure at foraging sites were more important in limiting breeding goshawks because vegetation structure appears to affect goshawks both directly and indirectly. Goshawks may be affected directly because they prefer older forest structures for nest sites, perhaps for protection from weather and predators, and a forest structure of tall trees and open understories that increases access to prey, and indirectly by affecting the distribution and abundance of prey.

Interactions among Factors

Essential to understanding how the factors reviewed here might limit goshawk populations is recognizing that these factors interact in complex ways at multiple spatial and temporal scales. We developed a schematic representation of the various pathways through which the limiting factors reviewed in this paper are likely to affect goshawk reproduction and survival (Fig. 2). Among-year variation in regional weather conditions leads to among-year fluctuations in forest productivity and, in turn, among-year fluctuations in goshawk prey populations. Among-year fluctuations in food abundance interact with forest structural conditions and weather, ultimately affecting prey availability and goshawk reproduction. The strength of these interactions are likely to depend on factors such as the number of species within the prey base, whether or not prey populations fluctuate in synchrony, spatial variation in the composition and structure of vegetation, and abundances of predators and competitors. Extreme weather events and disease can interfere with this flow of energy through the goshawk's food web by directly or indirectly affecting the physiological condition of goshawks, which, in turn, affects their reproduction and survival. The magnitude of competition, predation, and disease can also vary spatially or temporally depending on differences in food abundance, forest structure, and weather. The resulting changes in goshawk reproduction and survival contribute to the persistence of local populations, which in turn are regulated by dispersal within and among regional populations. When considered within the context of forest management (see Fig. 3 in Squires and Kennedy, *this volume*), our schematic provides a conceptual framework for understanding the causal pathways between these potential population limiting factors and goshawk viability.

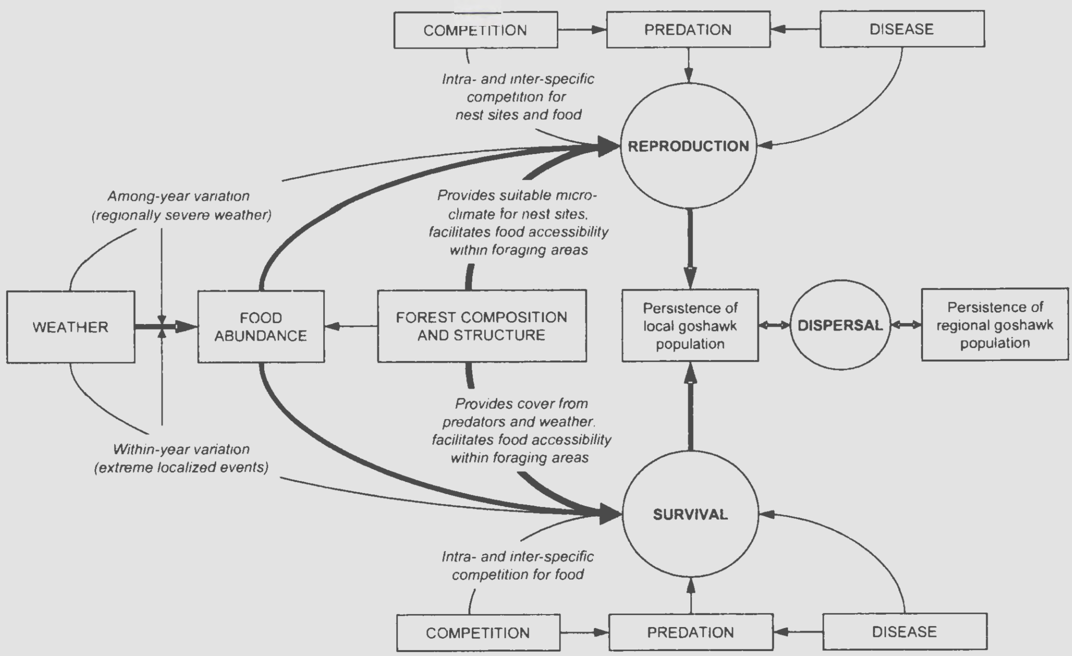

FIGURE 2. Schematic representation of the various pathways by which physical and biotic factors interact to limit Northern Goshawk vital rates and, ultimately, the persistence of local and regional breeding populations. Thicker lines indicate pathways with relatively stronger effects.

We propose that the additive effects of food abundance, forest composition and structure, and weather are much stronger than their individual effects on goshawk reproduction and survival. For example, if prey abundance is reduced by a period of environmental stress, goshawks may be unable to attain sufficient food to lay eggs. Alternatively, if prey abundance is high but goshawks cannot see or capture their prey because of unsuitable forest structure, they may have to change their hunting habitat, expand their foraging movements, alter their hunting behavior, or switch to alternate prey. Each of these changes could lower goshawk hunting efficiency. Lowered hunting efficiency, whether caused by low prey abundance or availability, can have an additional negetive effect on goshawk reproduction by causing females to leave their nests to help with hunting, thereby increasing the exposure of eggs or nestlings to predators (Newton 1986, Dewey and Kennedy 2001). Weather, predation, and competition may also play a even larger role when habitat is lost or degraded through natural or human disturbance. Finally, low food abundance or availability in forests may force adult goshawks in winter to leave for more open habitat where predation risks may be higher. Because of all the above, we argue that food abundance, vegetation structure and composition, and weather are likely to be the most ubiquitous factors limiting goshawk populations. We also argue that these factors, which often act in concert, are likely to mask the direct effects of forest management on goshawk vital rates in short-term studies.

Population Limitation and Natural Variation

Population limitation refers to a process that sets the equilibrium point (Sinclair 1989), or, more generally, a process that determines the stationary probability distribution of a population's density (Williams et al. 2002). Temporal and spatial variation in the operation of limiting factors may cause goshawk population densities to move around an average value. Some goshawk demographic parameters such as the proportion of pairs breeding, fecundity, juvenile survival, and recruitment appear to vary among years more than other parameters such as territory distribution, territory occupancy, and adult survival (Squires and Reynolds 1997, Andersen et al. 2004, Reynolds et al. 2004, Wiens et al. 2006a; Reynolds and Joy, *this volume*). Goshawk vital rates are closely tied to their food resources. Therefore, temporal variation in food abundance superimposed on spatial variation in food availability can be expected to generate substantial spatial and temporal variation in goshawk vital rates. Because short-term studies are not likely to detect the full range of natural variability in goshawk vital rates, and because an understanding of the extent and source of this variation is needed to tease-out the effects of forest management on the interactions among limiting factors, identifying the cause-effect responses of goshawks to management is necessarily a long-term endeavor.

Concluding Comments

We believe that the extent to which food, forest vegetation, predation, competition, disease, and weather affects goshawk populations can be mediated by providing suitable forest structure for goshawk nesting and foraging, as well as the habitats of a local suite of goshawk prey. Forest landscapes that include the habitats of the goshawk's prey (Reynolds et al. 1992; Drennan et al., *this volume*), forest structures that protect goshawks from weather and predators at nest sites (Reynolds et al., *this volume*), and forest structures that enhance the availability of prey to goshawks are more likely to sustain viable goshawk populations than forests lacking these features. An underlying issue in the debate over the status of the Northern Goshawk is the management of remaining old-growth forests (Peck 2000). However, we believe that the issue is broader than this and that a full understanding and recognition of the various natural factors that result in variation of goshawk demographic performance is the key to developing sound management strategies for goshawks and the forest ecosystems that they are dependent upon.

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