CAUSES OF DISPERSAL IN NORTHERN GOSHAWKS (*ACCIPITER GENTILIS*) IN FINLAND

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ABSTRACT.—Environmental quality has the potential to influence dispersal if cost of dispersing is outweighed by cost of staying. In that scenario, individuals experiencing different conditions in their natal area are expected to differ in their dispersal. Even if there is wide agreement that reasons behind the dispersal decision are multiple, it is often less clear what conditions actually add to the observed dispersal behavior. The scale at which the dispersal behavior is analyzed can also be of crucial importance for a correct understanding of the dispersal process. Furthermore, in long-lived species factors influencing dispersal behavior of juveniles may differ from those adding to dispersal of adults. Using 12 years of banding data (1989–2000), we studied dispersal behavior of Northern Goshawks (*Accipiter gentilis*) hatched over a wide area in Finland in relation to local demographic and ecological conditions. Hatching rank and hatching date added to the probability of leaving in the first place; whereas hatching date, local prey availability, and sex of the disperser were related to dispersal distance. Among adult birds (+3 years), none of the analyzed variables were related to distance; whereas the probability of remaining locally was related to local grouse density in the hatching year (for males only). Results show that the combined effects of factors working at several levels act together on dispersal behavior in Northern Goshawks and highlight the importance of studying different age classes separately in long-lived species. In summary, our results suggest that goshawk individuals distribute themselves spatially in parallel with factors determining the costs and advantages of dispersing where philopatry seems to be connected to factors positively associated with survival; but to test the validity of that idea, more data on fitness consequences of dispersal are needed. *Received 3 May 2002, accepted 14 December 2002.*

RESUMEN.—La calidad ambiental puede influir en la dispersión si el costo de ésta es superado por el costo de permanecer. En este escenario, se esperaría que los individuos que experimentan diferentes condiciones en su área natal difieran en sus patrones de dispersión. Aunque hay un consenso sobre la existencia de múltiples factores que afectan la dispersión, las condiciones específicas que influyen el comportamiento de dispersión son menos claras. También, la escala a la que se analiza el comportamiento de dispersión puede ser de gran importancia para un mejor entendimiento del proceso de dispersión. Además, en especies longevas, los factores que influyen la dispersión de los juveniles pueden diferir de aquéllos que afectan la dispersión de los adultos. Con información de 12 años de anillamiento (1989-2000), estudiamos el comportamiento de dispersión de *Accipiter gentilis* en un área de gran extensión en Finlandia con relación a las condiciones demográficas y ecológicas locales. El orden y la fecha de eclosión contribuyeron a la probabilidad de partir primero, mientras que la fecha de eclosión, la disponibilidad local de presas, y el sexo, estuvieron relacionados con la distancia de dispersión. Entre las aves adultas (+ 3 años), ninguna de las variables analizadas estuvo relacionada con la distancia, mientras que la probabilidad de permanecer estuvo relacionada con la densidad local de perdices en el año de eclosión (sólo en machos). Los resultados muestran que los efectos combinados de los factores que operan a diferentes niveles actúan conjuntamente en el comportamiento de dispersión de *A. gentilis* y demuestran la importancia de estudiar por separado a las diferentes clases de edad en especies longevas. Nuestros resultados sugieren que la distribución espacial de *A. gentilis* resulta de los factores que determinan los costos y ventajas de dispersión. La filopatría parece depender de los factores asociados positivamente con la sobrevivencia; sin embargo, para probar la validez de esta idea, se requiere mayor información sobre el impacto que las consecuencias de la dispersión tienen sobre la adecuación.

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Environmental quality is known to influence many important life-history aspects, such as survival and reproductive success (Lack 1968, Martin 1987, Clutton-Brock 1988, Newton 1998, Bennett and Owens 2002). Moving away from one location or deciding to remain can affect survival and reproduction because environmental quality normally varies in space and time (Parker and Stuart 1976, Clobert et al. 2001). Dispersal behavior, therefore, may potentially be affected by local environmental quality as estimated, for example, by number of competitors, territory availability, or availability of food. In that scenario individuals should seek better opportunities elsewhere if cost of dispersal, such as increased energy expenditure and increased mortality (e.g. Waser et al. 1994), is outweighed by cost of remaining behind. That, in turn, leads to a situation in which individuals experiencing different social and environmental conditions are expected to differ in their dispersal behavior (Arcese 1989, Pruett-Jones and Lewis 1990, Herzig 1995).

There is wide agreement that dispersal is a multicausal phenomenon (Clobert et al 2001), and even if focusing on possible environmentally determined dispersal only, it is seldom clear what specific environmental quality measurements are that add to the dispersal decision. The issue is complicated because of several factors. First, because species experience their environment very differently, on what basis the dispersal decision will be made is likely to be specifically related to the biology of the species in question (Clobert et al. 2001). Second, differences in dispersal need not be a result of factors working at one ecological level alone (e.g. landscape level, population level, individual level), but conditions at multiple levels may act together and have summed effects (Bengtsson et al. 1994, Léna et al. 1998). Those conditions may further be interrelated, causing confounding and interactive effects between them (Ims and Hjermann 2001). For example, in experiments with common lizards (*Lacerta vivipara*), body condition was found to interact with female density, dispersers showing better body condition than nondispersers at high female density (Léna et al. 1998). Third, decision to disperse might be affected by different factors than how far to disperse. Among birds in which that has been found to be the case are Black Kites (*Milvus migrans*; Forero et al. 1999) and Lesser

Kestrels (*Falco naumannii*; Serrano et al. 2001). Fourth, factors affecting the dispersal behavior of juveniles may differ from those that govern the dispersal behavior of adults, especially in long-lived species (Kenward et al. 2001).

Here, we examine the ecological and demographic factors related to the dispersal decisions made by juvenile (first-winter dispersal) and adult Finnish Northern Goshawks (*Accipiter gentilis*; hereafter "goshawk"), a medium-sized monogamous raptor distributed over large parts of the Palearctic and Nearctic regions (Cramp and Simmons 1980, Ferguson-Lees and Christie 2001). Although it is known that many juvenile Fennoscandian goshawks do not move far from their natal grounds during their first winter, other individuals move considerable distances, some juveniles even being variously migratory (Kjellén 1999). Reasons behind those individual differences in dispersal behavior of juveniles are not known. In contrast to juveniles, adult goshawks are more site-tenacious; and after settling they usually remain within or in the close vicinity of their territory all year (Widén 1985, Halley 1996). That pattern differs partly from patterns observed in North America (Alaska) where some female goshawks seem to move over longer distances than males (Flatten et al. 2001). Because of the differences in dispersal behavior between juveniles and adults, and because we were interested in determining whether conditions in the natal grounds have both short-term and long-term effects in observed dispersal behavior in goshawks, we analyzed juvenile and adult birds separately. Four questions concerning their dispersal were addressed: (1) which factors are related to the decision to stay or to leave the natal ground made by juveniles during their first winter; (2) what factors correlate with juvenile dispersal distance; (3) to what degree are conditions at the natal ground, if at all, reflected in dispersal probability and dispersal distances of birds later recovered as adults; and (4) are factors governing dispersal patterns of juveniles and adults similar?

Methods

Material on goshawk dispersal was obtained from the Finnish Ringing Center at the Finnish Museum of Natural History in Helsinki. In highly mobile species, use of banding material can be considered the best

available option for an analysis of dispersal because it overrides the main source of potential bias of dispersal estimates measured from local population studies (i.e. the limited size of study areas relative to the dispersal distance of the birds themselves; Newton and Rothery 2000). Furthermore, band recoveries and radiotag material have been shown to be equally reliable as information sources on dispersal (Walls and Kenward 1998).

After bird-banding activity was begun in Finland in 1913, a total of 44,562 goshawks were banded until late 2000, including all age categories, and of those 7,641 (17.1%) were later recovered (Saurola 2001). For reasons given below, we consider only nestlings banded in 1989–2000 and later recovered as dead, for which banding and recovery coordinates were known to at least the nearest kilometer. Because of possible estimate bias (see Kenward et al. 1999), birds that were shot and birds in which cause of death was unknown were excluded. Furthermore, condition of the recovered birds had to be such that the time of death could be assured within a one-week margin: long-decayed individuals were not accepted. Because we were not interested in studying postnestling dispersal (see Kenward et al. 1993a, b), we also excluded birds recovered before 1 October in their hatching year. For recoveries in which those requirements were fulfilled ($n = 571$), distance between banding site and recovery site was then extracted directly from the banding database.

All recoveries were then categorized into six different age classes on the basis of their absolute age at the time of recovery (first winter, second summer, second winter, third summer, adult winter, adult summer; winter: 1 October to 28 February, summer: 1 March to 30 September). Even if variation in banding activity between different regions leads to geographical variation in the number of goshawks being banded, most bandings occurring in the southern and western parts of the country (reflected in the geographical variation in the origin of recovered birds, Fig. 1), the exact brood size at the time of banding was known in almost all cases ($n = 561$). Thanks to sexual size dimorphism in goshawks (Ferguson-Lees and Christie 2001), sexing of nestlings at the time of banding is a reliable method (Byholm et al. 2002a), and because banders quite often report the sex of the individuals they handle, we had reliable information on the sex of the nestling in 377 cases. In nests where wing lengths of all nestlings in the brood were measured ($n = 283$), we were also able to calculate brood-specific hatching asynchrony rates (Burley and Calkins 1999) and hatching dates by backdating. Regarding nests where all nestlings were wing-measured, we also reconstructed hatching rank of the banded nestlings as intrabrood differences in wing length of nestling goshawks have been shown to correctly reflect individual hatching order (Bijlsma 1996). However, because sex, brood size, and wing
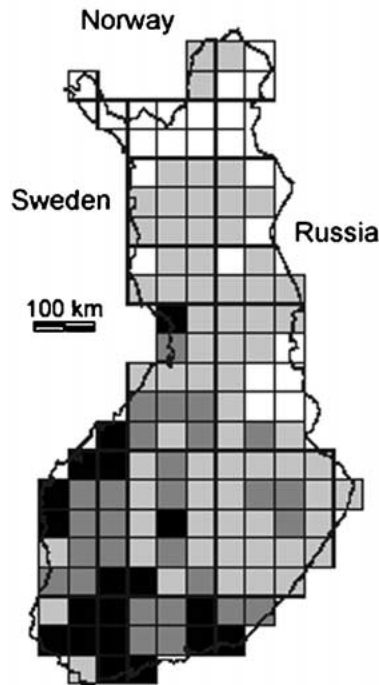

Fig. 1. Grids sized 50×50 km ($n = 115$) in which banded ≥1 of the Northern Goshawks in 1989–2000 later recovered [light gray: 1–9 recoveries (first 33%), dark gray: 10–23 recoveries (second 33%), black: 24–68 recoveries (third 33%)]. Unfilled grids ($n = 23$) lack recoveries of hawks banded therein.

length were not known for all recoveries, the number of cases that could be assigned all combinations of information was further reduced ($n = 272$).

Grouse are the most important prey for Finnish goshawks (e.g. Lindén and Wikman 1983, Tornberg 1997), and goshawks reproduce better in years with high grouse density than in years when grouse are in low abundance (Byholm et al. 2002b). (The grouse species involved are Capercaillie [*Tetrao urogallus*], Black [*T. tetrix*], Hazel [*Bonasa bonasia*], and Willow [*Lagopus lagopus*] grouse). Bearing that in mind, we calculated a local resource availability estimate using grouse census data for all natal areas involved (a set of objectively generated 50×50 km grids, Fig. 1). That was possible thanks to the wildlife triangle scheme, a census network used to assess autumnal grouse densities throughout Finland, originally meant for monitoring purposes and sustainable hunting (see Lindén et al. 1996 for details). That the scheme was initiated in 1989 was the reason why previous recovery data on goshawks were discarded (see above). Because populations of Finnish grouse fluctuate asynchronously both in space and time (e.g. Lindström et al. 1995,

Ranta et al. 1995), a relative measure of grouse—residual grouse density—was used instead of the absolute values as a measure on resource availability. Residual grouse density thus refers to values obtained from original grouse-data standardized to zero mean and unit variance (Sokal and Rohlf 1995). By using those relative grouse density values, the spatial asynchrony present in fluctuations of the grouse population could thus be compensated for.

Even if goshawks do not molt into complete adult plumage prior to the end of their third year of life (Ferguson-Lees and Christie 2001), many individuals begin to breed at younger ages (i.e. already in their second or third spring; Kenward et al. 1999, P. B. Byholm unpubl. data). Because of that stepwise recruitment of differently aged birds into the breeding population, we could not determine how many of the birds recovered as subadults had actually bred. Therefore, to keep the dispersal measures of breeding birds as conservative as possible, we did not include birds recovered prior to their third winter (>850 days of age) in the analyses of adult dispersal. Because of the inaccuracy of the recovery data, the measure of adult dispersal thus includes both natal and breeding dispersals, following the definitions of Greenwood (1980). Subsequently, the term "adult dispersal" refers to dispersal observed between the site where the bird was banded as nestling (the natal site) and the site where it was recovered dead as adult at least three years later. In light of present scientific results concerning site fidelity and migratory status of North European goshawks (e.g. Widén 1985, Halley 1996, Kjellén 1999) adult birds were assumed to be within or close to their breeding territory at the time of death. To that end, all remaining data regarding first-winter dispersal of juvenile birds (n = 135) and adults (n =19) were grouped into the 50×50 km grids on the basis of the banding coordinates. At that (grid) scale, by the use of banding data, we also calculated annual estimates on population-level sex ratio among offspring and mean productivity (nestlings to pair ratio) for all grids involved.

Statistical analyses.—General linear models (GLMs) were used to assess factors influencing probability of goshawks leaving their natal grid and, respectively, to determine what factors were significantly related to dispersal distance. Fitting a logit link function with binomial errors identified the factors affecting dispersal probability. After first log transforming the data on dispersal distances, we used a GLM with an identity link and normal errors to analyze which factors were associated with distance dispersed. Regarding GLMs on both dispersal probability and dispersal distance, we first fitted all factors (Table 1) univariately into a model without interactions, from which factors having P < 0.15 were selected and reanalyzed in a new set of models where all involved factors and their second-order interactions were fitted following a modified backward stepwise procedure yielding a minimum adequate model (Crawley 1993). That process was followed to avoid a too substantial reduction in the degrees of freedom. The GLM analyses were preformed with the MATLAB module Glmlab (see Acknowledgments) or SYSTAT (Wilkinson 1998). All other analyses were performed with SYSTAT.

RESULTS

Juvenile dispersal.—Irrespective of sex, goshawks hatched early in the season were more likely to remain in their natal grid than were their later-hatched conspecifics (Fig. 2A). Even though the effect was not significant (Table 2), the probability of dispersing also tended to be related to hatching rank, first-hatched nestlings within a brood (first-ranked) being less likely to leave the natal grid than their later-ranked siblings (Fig. 2B). If first-ranked nestlings consistently originated from broods assigned an earlier hatching date than their conspecifics belonging to later-ranked categories, that result could be nothing but an artifact. To ascertain whether that was the case, we tested if hatching dates differed between rank categories, and even if that actually were the case (ANOVA, F = 5.39, df = 2 and 132, P = 0.006), Tukey's *post hoc* test clarified that it was the last-rank category only (last-hatched) that was responsible for the significance (P < 0.05). In other words, birds ranked first do not hatch earlier—or later than—middle-ranked nestlings.

Regarding dispersal distance, we found that juvenile male goshawks disperse farther than females (median, males: 80.0 km; females: 34.5 km; see Table 3). In addition, early hatched birds remained closer to the natal site than later-hatched birds. However, because the interaction between sex and hatching date approached statistical significance (Table 3), that indicates that the relationship between hatching date and dispersal distance differed between males and females. If the sexes are analyzed separately, the relationship between date and dispersal distance is in fact significant among males; whereas the dispersal distance of females is unrelated to hatching date (Fig. 3). Irrespective of sex, dispersal distance is also related to local grouse density, juvenile goshawks remaining nearer to the natal site when local grouse density is high than when grouse are scarce (Table 3).

Adult dispersal.—Because of the statistical un-

TABLE 1. Factors fitted in GLMs, measured at the individual, brood, or grid levels.

Individual level

Sex

Hatching rank in brood (first, middle, last)

Brood level

Brood size (number of nestlings at time of banding)

Laying date (mean hatching date of brood)

Hatching asynchrony rate (hatching span [in days] /number of nestlings)

Grid level

Offspring sex ratio (proportion of males among nestlings banded in grid x in year t)

Mean productivity (mean number of nestlings banded in grid x in year t)

Residual grouse density ([grouse density in grid x in year t – mean grouse density in grid x in 1989–2000] /grid specific grouse density SD)

TABLE 2. Probability for juvenile Northern Goshawks to leave their natal grids (50×50 km) in their first winter as estimated by a backward stepwise GLM model with binomial error and logistic link function (stay coded as 0, leave as 1). Differences in the probability to leave the natal grid are apparent with respect to the laying date and hatching rank (first, middle, last). Factors and interactions not shown (cf. Table 1) were insignificant and deleted from the model.

Term	χ^2	β	(Δ)df	P
Constant	9.791	1.0437	1	0.001
Hatching date	9.516	0.1229	1	0.002
Rank	5.580	1.2650[a] 0.3293[b]	2	0.061
Error	140.452		131	

[a] Middle-ranked nestlings.
[b] Last-ranked nestlings.
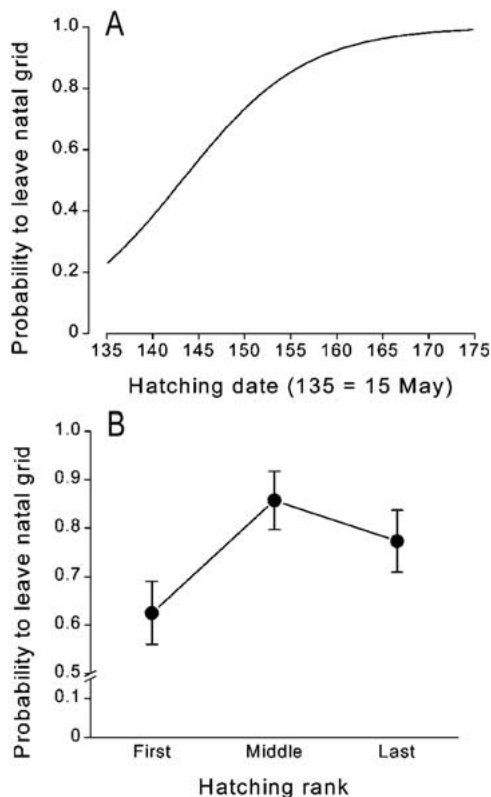
certainty related to small sample sizes in logistic regressions (Crawley 1993), we could not apply GLMs to the dispersal probability of adult goshawks because of the low number of degrees of freedom we had for the complete combinations of explanatory variables (see above). When reducing the number of variable combinations, the only model having a reasonable sample size left (n = 27) showed that the probability of adults dispersing from natal grid was equal for males and females (GLM, χ^2 = 0.56, Δdf = 1, P = 0.45) and that it was not related to local grouse density in hatching year as such (χ^2 = 1.37, Δdf = 1, P = 0.24). However, sex and grouse density interacted (χ^2 = 3.94, Δdf = 1, P = 0.05). When males and females were analyzed separately, we found that the probability for recovery outside the natal grid tended to vary in relation to local grouse density in adult goshawk males; whereas no clear relationship existed between dispersal probability and grouse density in females (Fig. 4A): males were recovered outside their natal grid more often if hatched during lean conditions rather than during good conditions.

Dispersal distance traveled by adults from the natal site (median, males: 49 km; females: 64 km) was not connected to brood size, sex, or grouse density in a GLM, and all other individual tests for explanatory variables (Table 1) were also nonsignificant.

Differences in dispersal between juveniles and adults.—When comparing dispersal distances between juveniles and adults and simultaneously, accounting for the effect of gender, neither

FIG. 2. Probability for juvenile Northern Goshawks to leave their natal grid (50×50 km) during their first winter in relation to (A) hatching date (function scaled to data range) and (B) hatching rank (first, middle, last; mean ± SE). Final model for (A): (logit/leave) = 6.014 + 0.124x.

TABLE 3. Factors affecting dispersal distance (log-transformed) of juvenile Northern Goshawks in their first winter as analyzed with a backward stepwise GLM having a normal error distribution and an identity link. Dispersal distance increases with late hatching date, a low relative grouse density, and males disperse further than females (females coded as 0, males as 1). In addition, the interaction between sex and hatching date approaches significance, males having a steeper seasonal slope than females (Fig. 3). Factors and interactions not shown (cf. Table 1) were insignificant and deleted from the model.

Term	F	β	(Δ)df	P
Constant	1231.151	4.417	1	<0.0001
Sex	10.480	0.316	1	0.003
Hatching date	9.399	0.047	1	0.005
Residual grouse density	9.125	−0.315	1	0.006
Sex × hatching date	3.056	0.027	1	0.105
Error	149.238		130	

effect of sex nor age improved the model alone; whereas their interaction was highly significant (backward stepwise GLM, age category-sex: F = 7.03, df = 1 and 243, P = 0.009). Because juvenile males disperse farther from the natal area than juvenile females (see juvenile dispersal, Table 3), that effect arises as adult males are recovered closer to the natal site than juveniles, whereas the opposite holds for females (Fig. 4B). Conversely, even if adults were somewhat more often recovered within the natal grid than juveniles, that difference was far from significant (χ^2 = 1.07, df = 1, P = 0.30); that is, both age classes showed the same relative degree of philopatry at the 50 × 50 km grid scale. Hatching dates also did not differ between juveniles and adults (*t*-test, t = 0.6, df = 152, P = 0.55).

DISCUSSION

Factors related to first-winter dispersal.— Hatching date was the most important factor related to the probability that juvenile goshawks leave their natal grid in their first winter. Late-hatched birds had a considerably higher probability of dispersal than their earlier-hatched conspecifics. Similar patterns of dispersal probability in relation to hatching date have been seen in local population studies on natal dispersal in some short-lived passerines (Dhondt and Hublé 1968, Drilling and Thompson 1988, but
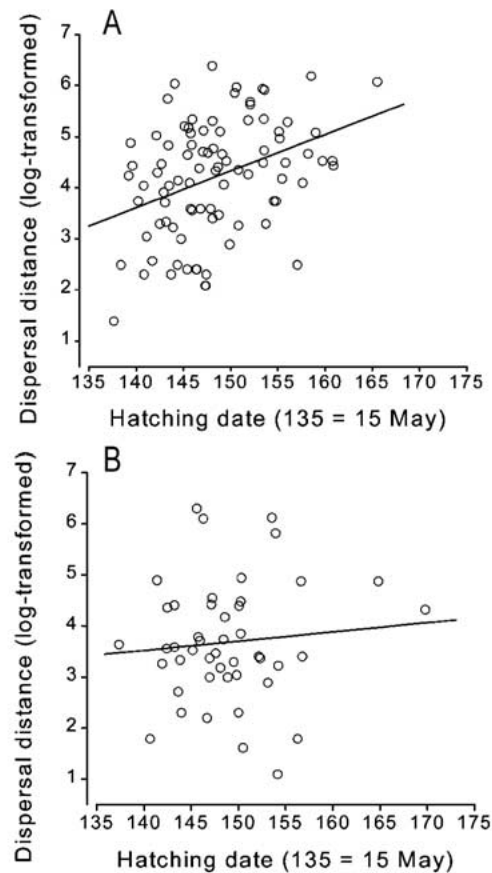

FIG. 3. Dispersal distance (log-transformed) of juvenile Northern Goshawk (A) males (*n* = 89) and (B) females (*n* = 46) in their first winter in relation to hatching date. Early hatched males disperse shorter distances than late-hatched males, whereas female dispersal distance is unrelated to hatching date. Final models, distance males: $y = 4.397 + 0.07x$, r^2 = 0.14, P < 0.001; distance females: $y = 3.721 + 0.018x$, r^2 = 0.01, P = 0.54.

see Verhulst et al. 1997, Altwegg et al. 2000), but to our knowledge our study is the first to show that the same pattern is prevalent in several sub-populations of a long-lived raptor. In addition to date, hatching rank was also related to probability of hawks leaving the natal 50 × 50 km grid, first-hatched nestlings within a brood (first-ranked) tending to remain local more often than middle- and last-ranked. Because first-ranked nestlings do not hatch earlier than those belonging to the middle-rank category on the population level, that result suggests that first-ranked nestling are more likely to remain
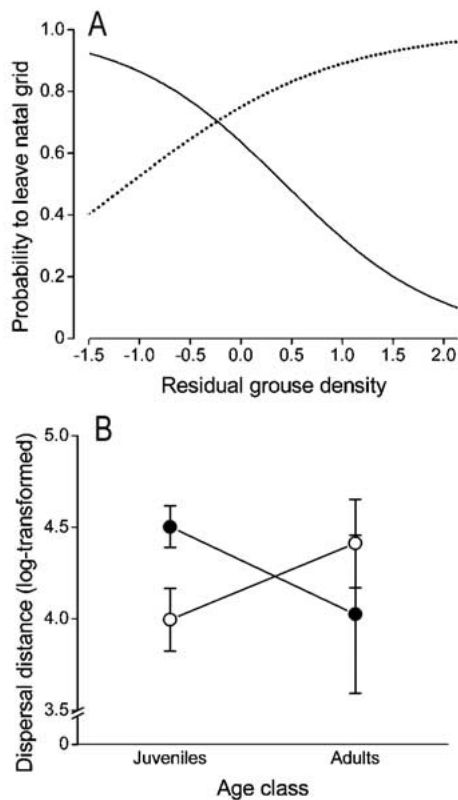
FIG. 4. (A) Probability of adult Northern Goshawks leaving their natal grid (50 × 50 km) in relation to local grouse density in hatching year. Probability of males (solid line) leaving tends to decrease as local grouse density increases (logistic regression, $\chi^2 = 2.72$, $df = 1$, $P = 0.1$; [logit/leave] = 0.560 – 1.294x); whereas grouse density does not affect adult female (dotted line) dispersal probability ($\chi^2 = 1.37$, $\Delta df = 1$, $P = 0.24$; [logit/leave] = 1.099 + 0.995x). Functions are scaled to data range. (B) Dispersal distance (log-transformed) ±SE of Northern Goshawks by age category and sex. Among males (filled circles), juveniles ($n = 146$) are recovered farther away from the natal site in their first winter (1 October to 28 February) than they are as adults (i.e. older than 850 days [+3 years], $n = 13$); whereas females (open circles) are recovered closer to the natal site in their first winter ($n = 67$) than they are as adults ($n = 21$).

within the natal grid than are their later-ranked siblings, irrespective of hatching date. That suggests that intrabrood dominance patterns (Boag and Alway 1980) add to the decision of whether to stay or leave made by juvenile goshawks, as observed in some other birds (Strickland 1991, Tonkyn and Plissner 1991, Forero et al. 2002).

Even if probability of leaving the natal grid in the first winter does not vary between the sexes in juveniles, juvenile males disperse further than juvenile females if dispersal is to occur, an effect that is especially clear among males originating from late-hatched broods (Fig. 2). Whether juvenile males and females differ in their dispersal is then dependent on the scale at which the phenomenon is studied (see also Verhulst et al. 1997), and also if factors other than sex alone are considered. The observation that juvenile males disperse farther than juvenile females can be considered to be in line with the obviously common pattern of male-biased movements among juvenile birds in northern raptors (Kjellén 1999), including goshawks (Haukioja and Haukioja 1970, Mueller et al. 1977, Halley 1996). However, it has not previously been shown that there is a difference between goshawk males and females in their response to hatching date, even if date and natal dispersal distance previously have been reported to correlate in some passerines, some raptors, and a larid (Dhondt and Hublé 1968, Nilsson 1989, Village 1990, Spear et al. 1998, but see Korpimäki and Lagerström 1988, Ferrer 1993). Interestingly, a pattern similar to the one found in goshawks was recently reported from analyses of banding data of Eurasian Sparrowhawk (*Accipiter nisus*): hatching date correlated positively with dispersal distance in males, but less clearly in females (Newton and Rothery 2000). Altogether, the observed pattern highlights the importance of accounting for factors other than only sex of the disperser for a correct understanding of the causes of dispersal. Dispersal of female and male birds does not necessarily differ solely in relation to sex, but ecological factors (hatching date in goshawks) may also be important.

In addition to hatching date, there was a negative relationship between dispersal distance and grouse density in the natal area. The effect was unrelated to sex, and both juvenile males and juvenile females dispersed shorter distances when local grouse density was high than when it was low. That is consistent with earlier findings in some other birds, including goshawks, in which food availability in the natal area—even if estimated only indirectly—was related to the dispersal distance in young-of-the-year (Kenward et al. 1993b, Adriaensen et al. 1998). Furthermore, the importance of food was also highlighted in explaining the dispersal

of young Song Sparrows (*Melospiza melodia*), because food supplementation increased the rate of philopatry in experiments with that species (Arcese 1989).

In summary, results indicate that there may be a limit to how many goshawks a certain area (grid) can host and that the observed patterns are a result of late-hatched or high-ranked birds being forced to leave the natal area through an ideal despotic distribution process, where early birds (early-hatched in relation to date and first-ranked) are in a superior position in the competition for local winter territories (cf. Murray 1967, Greenwood 1980). Over a wider scale, dispersal is also related to local grouse density, indicating that the competition is less strong when grouse density is high than when grouse density is low. Combined, those results are in line with theoretical models demonstrating that competition for resources is the primary force driving dispersal in birds and mammals, residents being able to displace nonresidents (Waser 1985, Tonkyn and Plissner 1991). From the hawks' point of view, competition for space can also be considered a "scaling process." Probability of dispersal among juveniles is a sum of characteristics of the individual (hatching rank) and conditions characterizing the entire brood (hatching date); whereas dispersal distance traveled by juveniles in their first winter is related to both individual characteristics (sex), to characteristics related to the brood (hatching date), as well as to factors working at the landscape level (local grouse density).

Differences in the dispersal pattern of juveniles and adults.—Our limited sample on adult dispersal showed that adult males tended to be recovered within the natal grid more often if they were hatched in a year when local grouse density was high than when it was low. Probability of females being recovered within the natal grid was not affected by local grouse density in the hatching year. That result is not in direct concordance with the result on juvenile dispersal (see above): juvenile males dispersed over clearly longer distances than females if hatched from late broods; whereas dispersal distance of both juvenile females and juvenile males was shorter when local grouse density was high than when it was low. Because the difference in dispersal distance is lacking in adults, it is the dispersal distance of males that becomes shorter with age (Fig. 4B). Assuming

that our measure on adult dispersal correctly reflects natal (and breeding) dispersal in goshawks, that result suggests that goshawk males are the philopatric sex, an interpretation that is in contrast to earlier conclusions concerning natal dispersal in goshawks, but is in line with the general pattern seen in most birds, including raptors (reviewed in Greenwood 1980, Clarke et al. 1997). That discrepancy between our present findings and earlier conclusions regarding sex differences in philopatry (Clarke et al. 1997, but see Widén 1985) is likely a result of the fact that natal dispersal in goshawks breeding in northern latitudes has been interpreted previously from data originating from young birds in their first winter (Kenward et al. 1993b), whereas the majority of goshawks begin to breed at three years or older (Kenward et al. 1999). Therefore, to make correct conclusions for dispersal patterns in long-lived species, it is important to analyze patterns of juveniles and adults separately along the entire life path (cf. Kenward et al. 2001).

Whether males recovered as adults represent a subsample of birds remaining in their original natal grid, or whether they returned there as adults, is something we cannot determine on the basis of our data. However, because proportion of philopatric juveniles and adults does not differ at the grid scale, and because hatching dates of juveniles and adults are identical, (date being the main force affecting juvenile male dispersal distance) the latter explanation seems likely. That is also exactly what has been observed in at least three other raptors with long prebreeding periods. Subsequently, in the Common Buzzard (*Buteo buteo*; Walls and Kenward 1998), the Red Kite (*Milvus milvus*; Newton et al. 1994), and the Black Kite (Forero et al. 2002), birds seek to breed near their natal areas as adults even if they prospect over wider areas before beginning to breed.

The reason why males appear to return to the natal grid as adults is an interesting detail that we wish to further address. One possibility is that that behavior somehow is related to inbreeding avoidance (Pusey 1987, Perrin and Goudet 2001). Conversely, Forero et al. (2002) suggested that inbreeding avoidance is not the prime factor driving dispersal in species with high adult survival and juvenile mortality, delayed maturity, and high mate and territory fidelity—demographic patterns typical for

goshawks (Cramp and Simmons 1980, Squires and Reynolds 1997, Kenward et al. 1999). It has also been suggested that short-time reaction decisions (behavioral flexibility) may be the dominant strategy in an erratic environment (Ims and Hjermann 2001) characterized, for example, by severe fluctuations in food supply. The observation that intrabrood patterns (hatching rank) influenced dispersal probability only moderately suggests that dispersal in goshawks is not primarily a result of inbreeding avoidance, but our data set does not allow for more robust testing of that question.

Beyond inbreeding, it is possible that the tendency for adult males to be the philopatric sex is a function of philopatry being more advantageous to males than to females by means of enhanced nest-site acquisition, survival, or reproductive success. That has been documented in several other bird species (e.g. Pärt 1995, Bensch et al. 1998, Wheelwright and Mauck 1998, Forero et al. 2002, but see Spear et al. 1998). In goshawks, a higher degree of male philopatry may be related, for example, to the fact that the sex roles of goshawks distinctively differ. Goshawk males defend territory against adjacent males and are primarily responsible for provisioning females and young with prey (Squires and Reynolds 1997); whereas females are responsible for most of the parental care (Cramp and Simmons 1980). Accordingly, because grouse appear to be more important as a food source for goshawk males—especially in winter—than they are for females who have a broader prey spectrum (Tornberg and Colpaert 2001), philopatry could be especially advantageous for males because of payoffs related to high familiarity with natal area. Such payoffs include possession of a territory (see Widén 1985). In that scenario, territory possession and other philopatry-related advantages would be especially profound in times of high local grouse density, because adult males mainly are present more often in grids with high grouse density in the hatching year. Goshawk females, being less dependent on grouse and playing secondary roles in feeding young, may gain less from being philopatric. Consequently, philopatry seems to be in parallel with factors positively related to survival and reproductive success, both temporally and spatially; but before being able to test the validity of that hypothesis, further information

clarifying the relationship between dispersal and fitness is needed.

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Associate Editor: C. Marti