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Immediate Species Responses to Catastrophic Natural Disturbances: Windthrow Effects on Density, Productivity, Nesting Stand Choice, and Fidelity in Northern Goshawks (*Accipiter gentilis*)

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ABSTRACT.—In December 1999, an exceptional windstorm traveled across northern France (Côte d'Or). The severity of the stand damages ranged from <1 to >80%, and over 10% of the overall surface of several homogeneous woodlands (from ~1,000 to 8,000 ha) was affected by the windstorm. Data were available on Northern Goshawk (*Accipiter gentilis*) density, productivity, and nesting stand preferences in that area before the disturbance. The species showed tolerance to the natural disturbance induced by the windstorm: we found no difference in density, nesting stand choice, or productivity between the six breeding seasons before the windthrow and in the one immediately after. Breeding pairs moved away (50–200 m) from their traditional nest stand only when its original structure was altered by >30% in the 50 m surrounding the nest tree. We hypothesize that the Northern Goshawk tolerance to windstorm damage may be the result of an adaptive response, which they have developed under both climate- and human-originated stresses.

RÉSUMÉ.—En décembre 1999, une tempête de vent exceptionnelle a traversé le nord de la France (Côte d'Or). La sévérité des dommages portés aux arbres variait de <1 à 80%, et plus de 10% de la surface totale de plusieurs boisés homogènes (de ~1,000 à 8,000 ha) ont été affectés par la tempête. Des données concernant la densité, la productivité et les préférences du site nidification de l'Autour des palombes étaient disponibles (*Accipiter gentilis*) dans cette région avant la tempête. L'espèce s'est montrée tolérante aux dérangements de type naturel causés par la tempête: nous n'avons trouvé aucune différence dans la densité, le choix du site de nidification ou la productivité entre les six saisons de nidification avant la tempête et celle immédiatement après. Les couples nicheurs ont quitté (50–200 m) leur lieu traditionnel de nidification seulement dans le cas où la structure d'origine était altérée de >30% dans les 50 m autour du nid. Nous avons émis l'hypothèse que la tolérance de l'Autour des palombes aux dommages de la tempête pourrait être le résultat d'une réponse adaptative qu'ils auraient développée suite à des stress d'origine climatique et humaine.

All naturally occurring and human-disturbed ecosystems are mosaics of environmental conditions, and a large part of that heterogeneity arises from disturbances operating at various temporal and spatial scales. A disturbance may be defined as any relatively discrete event in time that may take place on a variety of spatial scales; that disrupts the ecosystem, community, or population structure; and changes resources, substrate availability, or physical environment (Pickett and White 1985). We refer to ''catastrophic disturbance'' as an event that occurs so rarely in a given geographic area that it is unlikely to be experienced as a repeated, selective force

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(Harper 1977). Species respond differently to disturbances depending on their ability to exploit disturbed patches, and individual responses may produce changes that are recognizable at the population level: attributes such as density, spatial distribution, mortality and reproductive rate may change (Karr and Freemark 1985).

Major natural disturbances, such as windstorms, have mainly been studied from the standpoint of plant species and systems: few authors have focused their attention on the response of animal species (White and Pickett 1985), and a small number of studies have compared some ecological attributes of a species before and after a disturbance (e.g. Dunning and Watts 1991, Lens and Dhondt 1992, Jones et al. 2001). Interest in natural disturbances stems from their fundamental implications in conservation biology and ecology (e.g. habitat fragmentation, dynamics of biological systems, alteration in reproductive output and nesting place; Pickett and White 1985).

On 26–28 December 1999, a storm considered exceptional in terms of magnitude intensity (wind speed of 80–173 km h^{-1}) and severity swept northern France (from Brittany to Burgundy), from west to east along the 49th parallel, over a path >150 km wide. Winds were accompanied by local rain and snowfalls. The windstorm developed from a deep depression of ~960 hPa, and the exceptional wind speed was the result of the interaction between the depression approaching land and the 400 km h^{-1} jet stream at 9,000 m altitude. In the Côte d'Or area (Burgundy region, eastern France), forest damage was concentrated in the north: the severity of the stand damage was very variable, ranging from <1 to >80%, and over 10% of the overall surface of several homogeneous woodlands (from about 1,000 to 8,000 ha) was affected by the windstorm (Office National des Forêts unpubl. data). The stand damage observed in the Côte d'Or forests exhibited a positive relationship with stand age and height, and a negative relationship with stand density; complete damage occurred only in stands of ≥100 years of age (Office National des Forêts unpubl. data).

The nesting stands of the Northern Goshawks (*Accipiter gentilis*) were particularly affected by that catastrophic event because they nest in the more mature stands of forests characterized by tall trees and high canopy cover (Penteriani 1999a, Penteriani et al. 2001), two elements that increase the stand vulnerability to windthrow (Foster 1988). Detailed data were available on density, productivity, and nesting stand preferences in the area hit by the windstorm for the six years preceding it (Penteriani 1999a). Consequently, we were able to examine the effects of the windthrow on (1) density of breeding pairs; (2) choice of a new nesting stand under the double pressure of the natural disturbance and of the starting of a new reproductive season; (3) productivity (expressed by egg-laying date, number of young per breeding pair and per successful pair); and (4) nesting stand fidelity (what severity of stand structure disturbance led a pair to move away and how far it moved).

Study area and methods.—We evaluated the immediate response of Northern Goshawks to the December 1999 windstorm from January to July 2000, in a forested area of the Côte d'Or of ~700 km^2. Wide and homogeneous tracts of broad-leaved trees (*Quercus pedunculata*, *Q. petraea*, *Fagus sylvatica*) with occasional small areas of cropland dominate the area.

Density was estimated by the nearest-neighbor distance method (NND; Newton et al. 1977), and regularity in nest spacing was tested by the *G*-test of Brown and Rothery (1978). Listening sessions of spontaneous, dawn and morning vocalizations of adults (Penteriani 1999b) were performed during the prelaying period (January–March in our study area) to identify the (new or traditional) stands occupied by a breeding pair after the windstorm. That method has the triple advantage of detecting the presence of breeders in their nesting site (1) with an efficiency of 100%; (2) very early in the breeding season; and (3) with the supplemental information on whether the stand is occupied by a pair or by a single bird only (Penteriani 1999b). A traditional nest stand is a stand where, in the six years preceding the windstorm, a Northern Goshawk pair attempted nesting, successfully or not, without moving away to a possible alternative nesting site. We evaluated the severity of the windthrow damage to the nesting stand structure by estimating by eye the percentage of fallen trees on two spatial scales: 50 m (the minimum area of mature stand required by the species to select it as a nesting site; Penteriani and Faivre 1997, Penteriani 1999a) and 500 m of radius around the nest tree.

We assessed the effect of the windthrow by testing (*t*-test) for possible differences in structure between the nesting stands, before the windstorm (n = 19), and the new ones chosen in the reproductive season after the windstorm. In the latter case, only the traditional nesting sites (n = 6) from where the pairs moved away because of the windstorm-induced alteration of the original stand structure were considered. We used 4 and 6 variables to describe the nest tree and the nesting stand, respectively: diameter at breast height (DBH), height and crown volume of the nest and stand trees, mean distance between the nest tree and nearest surrounding trees, mean distance between stand trees, stand canopy cover and flight space (for the description and computation of the above variables, see Penteriani and Faivre 1997). The selected variables—that is, those most commonly used in the analysis of Northern Goshawk nesting habitats (Bosakowski 1999, Penteriani 1999a)—also proved to be important in the description of the nest site structure (Penteriani and Faivre 1997, Penteriani et al. 2001). Characteristics of the nesting stand in-

TABLE 1. Comparison (t-test) of the structure ($\bar{x} \pm$ SD) of Northern Goshawk nesting stand before (n = 19) and after (n = 6) the windthrow.

	Before windthrow	After windthrow	t-test	P
Nest tree characteristics				
Diameter at breast height (m)	0.49 ± 0.1	0.48 ± 0.1	0.135	0.89
Height (m)	26.1 ± 4.2	26.2 ± 3.8	−0.032	0.97
Crown volume (m^3)	3665.9 ± 1427.0	3658.7 ± 998.3	0.007	0.99
Distance from surrounding trees (m)	7.7 ± 2.3	7.4 ± 1.4	0.334	0.74
Nest stand tree characteristics				
Diameter at breast height (m)	0.21 ± 0.1	0.16 ± 0.1	0.938	0.36
Height (m)	31.4 ± 8.2	33.5 ± 6.2	−0.567	0.58
Crown volume (m^3)	3442.4 ± 2121.6	2566.1 ± 925.5	0.972	0.34
Tree distances (m)	5.8 ± 2.1	7.7 ± 2.1	−1.881	0.07
Canopy cover (%)	91.4 ± 3.7	91.3 ± 4.2	0.020	0.98
Flight space (m^3)	70.0 ± 29.3	76.6 ± 21.8	−0.506	0.62

side a plot of 1 ha around the nest tree were measured. The Mann-Whitney U-test was used to identify possible differences in productivity (number of fledged young per breeding pair and per successful pair): (1) between the pairs (n = 19) reproducing before the windthrow (as the number of years during which each nest site was monitored was different, we used the mean number of young to avoid pseudoreplications) versus pairs reproducing in the breeding season after the windthrow, and (2) between the pairs (n = 13) that reproduced in their original stands after the windthrow, and the pairs (n = 6) that moved to a new stand for breeding, after the windthrow-induced damage. A mixed-model analysis of variance (ANOVA) was used to test for differences in the number of young per breeding pair and egg-laying date, before the windthrow and in the reproductive season immediately after the windthrow, for the same nesting stand (n = 19). In the mixed-model ANOVA (model III; dependent variables = productivity and egg-laying date), the windstorm was considered as the fixed factor (dichotomous variable: 0 = no windthrow, 1 = windthrow), and the nesting stand as the random factor (Sokal and Rohlf 1995).

TABLE 2. Comparisons of Northern Goshawk productivity parameters ($\bar{x} \pm$ SD, n; Mann-Whitney U-test) before and after the windthrow.

	Before windthrow	After windthrow
Young per breeding pair	1.7 ± 0.4 (n = 19)	1.5 ± 1.2 (n = 19)
	$z = -0.36$, $P = 0.72$	
Young per successful pair	1.9 ± 0.4 (n = 19)	2.2 ± 0.6 (n = 13)
	$z = -1.68$, $P = 0.09$	
Young per breeding pair	(in traditional stands)	1.4 ± 1.3 (n = 13)
	(in new stands)	1.8 ± 1.0 (n = 6)
	$z = -0.65$, $P = 0.51$	
Percentage successful pairs	78.9	68.0

When data were not normally distributed, they were $\log_e$ transformed, square-root transformed, or arcsine-square-root-transformed as necessary (Sokal and Rohlf 1995). All the means are given with ±SD, all tests are two-tailed, and statistical significance was set at $P < 0.05$. We used the SPSS (Chicago, Illinois) 10.0 software package.

Results.—The minimum distances between breeding pairs, prior to the windstorm, averaged 2.8 ± 0.58 km, and the values of 0.98 for the G-test indicated a regular distribution of nests within the study area. The pre-windstorm density was equal to 6.7 breeding pairs per 100 km^2 (Penteriani 1999b). The minimum distance between breeding pairs in the season following the windstorm averaged 2.7 ± 0.6 km, and the values of the G-test and density were the same as those recorded until 1999.

No significant difference was detected in stand structure between nesting stands chosen before and immediately after the windstorm (Table 1).

No difference was detected either between pair productivity values before and in the breeding season following the windthrow or between the pairs reproducing in their original stands and ones that moved to a new stand for breeding after the windthrow (Table 2). When considering the same nesting stand before and after the windstorm, we found no difference in number of fledged young per breeding pair ($F = 0.17$, df =1 and 50, $P = 0.69$) or in the egg-laying date (last week of March to the second week of April: $F = 0.85$, df = 1 and 50, $P = 0.36$).

With regard to percentages of stand damage recorded in the 19 nesting stands affected by windthrow, we observed that pairs (n = 6) moved away to reproduce only when the original stand structure was altered by >30% in the 50 m surrounding the nest tree. In stands where multiple nests were present, the pair always chose the one surrounded by forest with the least percentage of damage (≤30%), even if it differed from the one used in the preceding reproductive seasons. Higher percentage of stand damage in the 500 m surrounding the nest tree never caused a departure of the pair from the traditional nest stand if the damage in the 50 m around the nest tree was <30%. The only case in which a Northern Goshawk pair tried to reproduce in a stand with >30% of damage in the 50 m around the nest tree (50% in the 50 m, and 60% in the 500 m) failed after egg-laying, but the cause was impossible to determine.

As to the pairs that moved away after alteration of >30% of the original stand structure, in four cases (66.7%) the pairs moved to the nearest neighboring stand portion (50–70 m) not affected by the windstorm or altered by <30% and, in two cases (33.3%), the pair moved to a stand located >50 m away from the original (70 and 200 m), that is, at the borderline between the damaged stand and the undamaged one. In three out of the six above-cited cases, stand alteration also coincided with nest tree destruction.

Before the windstorm, no breeding failure had been observed to result from the lack of a mate in the pair (V. Penteriani unpubl. data). For the first time, in the reproductive season following the storm, we recorded the presence of a lone female in each of three traditional nesting stands (50% of the breeding failures). Those females—as opposed to the relatively silent ones that incubate (Penteriani 2001)—continued their vocal activity throughout the incubation period, giving the alarm call when intruders came into their nesting stand near the latest active nest.

Discussion.—Two complementary approaches may be taken when studying the effect of disturbances on vertebrates. First, we measure and evaluate the effect of a given disturbance; second, we analyze the immediate responses of vertebrates and interpret them in the context of past disturbance regimes, of either natural or anthropogenic origin. Both of these approaches concerning response to such a drastic environmental stochasticity might give useful conservation and management information: the understanding of internal mechanisms and external influences contributing to changes in a population and of how they interact provide a basis for building models for conservation and wildlife management (Starfield and Bleloch 1991).

The assimilative and adaptive capacity of a species determines its responses to disturbances and the effects of such disturbances on its behavior and ecology: the fitness of a species is not predetermined, it is the result of its evolution under a combination of natural and artificial, local constraints. In this context, different populations of the same species can react differently when they are exposed to different environmental and biological pressures (Pickett and White 1985, Mönkkönen and Welsh 1994, Kenward 1996).

The Northern Goshawk population in our study area showed tolerance to the natural disturbance due to the windstorm in the breeding season immediately after the catastrophic event: nest stand selection showed similar values under both undisturbed and disturbed landscape conditions, and all the investigated parameters of density and productivity displayed fairly similar values before and after the disturbance. The lower percentage of successful pairs was due to the high mortality recorded among males after the storm, with no precedent in the six years prior to the event. A direct effect of the windstorm on our population could explain the higher mortality rate of individuals, hidden by territory reoccupancy by ''floaters,'' but that was not actually detected during our study. Nevertheless, we think it is important to underline that our results only concern the immediate response of the species to the windthrow. Actually, there may be a time-lag in response, for example possible effects on fecundity could appear later when prey population have had time to respond to windfalls.

With regard to nest stand occupation and the observed short-distance movements after a severe stand structure disturbance, we can conclude that breeding pairs showed long term fidelity to their nesting stand, as long as the cover reduction did not exceed the above-mentioned threshold. The removal of >30% of the original tree cover increases the risks of predation and exposure to adverse weather conditions, therefore inducing individuals to leave their nesting stand (Robinson et al. 1995, Kenward 1996).

Prior analyses of the stand structure (Penteriani and Faivre 1997, Penteriani et al. 2001) revealed that nests are always found in the most mature portion of a tall tree stand, the size and distinctive features of which decrease with distance from the nest (50 m away from the nest tree, the stand structure has already changed). These structural data, combined with the responses of the species to the natural disturbance, highlight that the mature portion of the stand necessary for successful reproduction is limited in space (~1 ha). Northern Goshawks also appear to reproduce successfully if the disturbance-induced damage is below the 30% threshold in the nest surroundings or far from the 1 ha ''buffer'' zone around the nest, provided that it does not occur during the reproductive season.

Historically, ecologists have been slow to recognize the importance of disturbances to species and to the heterogeneity that they generate. The notion of a presumed natural equilibrium (climax) of biological systems, the fact that disturbances are regarded as exceptional events (rather than as extremes on a gradient of disturbance intensities), and that variability is often assumed to reflect noise or sampling inefficiencies (rather than real dynamics of biological systems), are the key factors responsible for the slow progress in this area (Karr and Freemark 1985). In larger ecological contexts, the adjustment of this European population of Northern Goshawk to catastrophic natural disturbances may be part of a wider process of adaptation of Palearctic species started during the disturbances of Pleistocene glaciations, which were characterized by long timescales, high severity, and large extent within the European continent (Mönkkönen and Welsh 1994). Additionally, our Northern Goshawk population was submitted to strong human-induced alteration (e.g. logging) for several centuries, as were the majority of the European populations. Penteriani and Faivre (2001) showed that the species can tolerate well the first two steps of regeneration felling that characterize the shelterwood system, moving away from their traditional nesting stand only when the windthrow damage exceeded the threshold of 30%. We hypothesize that the tolerance to windstorm damage may be an adaptive response, which this species has been developing under both Pleistocenic and long-term anthropogenic disturbances.

The response of this population has fortunate implications for management. It implies that populations stressed by long timescale disturbances seem to react well today to natural stochastic events. This population could represent a unique example of how long-term perturbations might ''prepare'' the individuals to better face unpredictable catastrophic events that affect the population dynamic in a stochastic way. This could be particularly important in the present situation in which global climatic change may determine more and more future catastrophic events.

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Investigation of Interacting Effects of Female Age, Laying Dates, and Egg Size in Yellow-eyed Penguins (*Megadyptes antipodes*)

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Abstract.—Increased experience with age may allow long-lived seabirds to forage more efficiently and ultimately to invest more into reproduction. In many seabirds, egg size increases with female age, but declines with laying date. Declines in laying date might be due either to quality of individual females or females may adjust their egg size in response to poorer conditions typically found late in the season. We investigated the influence of female age, date of laying, and annual variation on egg size in Yellow-eyed Penguins (*Megadyptes antipodes*). Further, we tested whether there was an effect of individual females or female age on date of laying. Whereas female age influenced egg volume, mass, and width, laying date had no effect on egg size or mass in Yellow-eyed Penguins. Laying dates differed significantly among females but were not affected by their ages. These results indicate that in Yellow-eyed Penguins, some individual females lay consistently early or late, regardless of age, but that egg size generally increases with age.

Resumen.—La mayor experiencia obtenida con la edad puede permitir a las aves marinas longevas forrajear con mayor eficacia y en última instancia, invertir más en la reproducción. En muchas aves marinas el tamaño de los huevos aumenta con la edad de la hembra, pero disminuye con la fecha de la puesta. La disminución del tamaño con la fecha de la puesta puede deberse a la calidad de cada hembra o a que las hembras pueden ajustar el tamaño del huevo en respuesta a condiciones más pobres típicas de los periodos más tardíos de la estación. Investigamos la influencia de la edad de la hembra, la fecha de puesta y la variación anual sobre el tamaño del huevo en los pingüinos *Megadyptes antipodes*. Además, probamos si había un efecto a nivel de cada hembra o de la edad de la hembra sobre la fecha de puesta. Aunque la edad de la hembra influyó sobre el volumen del huevo, la masa, y el ancho, la fecha de puesta no tuvo un efecto sobre el tamaño o masa del huevo en *M. antipodes*. Las fechas de puesta difirieron significativamente entre las hembras pero no fueron afectadas por las edades de éstas. Estos resultados indican que en *M. antipodes*, algunas hembras ponen consistentemente temprana o tardíamente en la temporada, independientemente de su edad, pero que el tamaño del huevo generalmente aumentó con la edad.

Several studies have found interacting effects of female age and laying date on egg and clutch size in seabirds that breed in seasonal environments: egg and clutch size increase with female age, but decline with laying date (e.g. Coulson and White 1958, Nelson 1966, Furness 1983). Two competing hypotheses have been developed to explain declines in clutch and egg size with laying date (Winkler and Allan 1996). Decrease in egg and clutch size might be due either to the quality of individual females, whereby poorer quality females (those less able to devote resources to egg production) lay small eggs as well as clutches late in the season, or females may adapt their clutch size to the poorer conditions typically found late in the season (Birkhead and Nettleship 1982). Although in some species egg and clutch size seem to be driven by laying date (with older females producing small clutches or eggs if they lay late), in other species age affects laying date as well as egg and clutch size, with older females tending to lay earlier and to lay larger eggs and clutches (e.g. Hamman

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