J. Field Ornithol., 68(4):607–612

THE EFFECTS OF PREDATION RISK ON SCANNING AND FLOCKING BEHAVIOR IN DUNLIN

ANDRES BARBOSA[1]
Departamento de Ecología Evolutiva, CSIC.
Museo Nacional Ciencias Naturales
C/José Gutierrez Abascal, 2
28006 Madrid, Spain

Abstract.—Dunlin (*Calidris alpina*) scanning and flocking behavior was studied in two habitats with different predation risk. Mean flock size, time spent scanning, and mean scan duration were higher in rice fields (the less profitable and high-risk habitat) than in littoral habitats (the more profitable and low-risk habitat), although vigilance rate was not different between habitats. Increased scanning and flocking behavior probably increase efficency in predator avoidance. The results are explained as behavioral changes to ensure safety in a high predation-risk situation when starvation risk is also present.

EFECTOS DEL RIESGO DE DEPREDACIÓN EN EL COMPORTAMIENTO DE VIGILANCIA Y TAMAÑO DEL GRUPO EN *CALIDRIS ALPINA*

Sinopsis.—Se estudió el comportamiento de vigilancia y el tamaño de grupos de *Calidris alpina*, en dos hábitats con diferente riesgo de depredación y diferente rentabilidad alimentaria. Los resultados muestran que el tamaño medio del grupo, el tiempo total de vigilancia y el tiempo medio de cada vigilancia, fue más alto en el arrozal (hábitat menos rentable y con más riesgo) que en el litoral (el hábitat más rentable y con menos riesgo). Sin embargo, la tasa de vigilancia no fue diferente entre los dos tipos de hábitats. Se ha señalado el incremento en los valores de las variables relacionadas con la vigilancia y el incremento del grupo como modo de aumentar la eficacia antidepredatoria. Los resultados obtenidos se explican como cambios en la conducta que incrementan la seguridad en una situación de alto riesgo de depredación coincidente con un alto riesgo de muerte por inanición.

Wintering birds should maximize their probability of surviving to the next breeding season (Caraco 1979). Survival depends on foraging efficiency and avoidance of predation. Habitat patches may vary both in foraging profitability and predation risk, so a forager must trade energy gains against the risk of predation when deciding where to feed (Suhonen 1993). On the other hand, competition (inter- and intraspecific) is known to affect foraging-site selection in birds (Alatalo 1982) by restricting individuals' use of more profitable habitat patches.

Animals often use low-risk patches even though safe areas are less energetically profitable (Anderson 1986, Caldwell 1986, Fergurson et al. 1988). At the Ebro Delta in Spain, Dunlin (*Calidris alpina*) forage in both littoral habitats and rice fields, prefering the more profitable littoral areas (Barbosa 1994, 1996). The use of rice fields, the less profitable habitat, seems to be a consequence of the temporal unavailability of feeding areas and density-dependent effects related to starvation risk (Barbosa 1996). However, predator density is higher in rice fields than in littoral habitats (Tombal and Tombal 1988). Raptor predation has been shown to be an

---

[1] *Current address: Laboratoire d'Ecologie, CNRS-URA 258, Université Pierre et Marie Curie, Bât. A, 7e etage, 7 quai St., Bernard, Case 237. F-75252 Paris Cedex 05. France.*

important source of mortality in wintering shorebirds (Creswell and Whitfield 1994, Page and Whitacre 1975). This allows an excellent opportunity to study anti-predator behavior such as flocking and scanning, when behaviors that lessen the risk of starvation may entail an increased risk of predation (Lima and Dill 1990, Weissburg 1986).

It is well established that birds benefit from feeding in flocks. Many shorebirds species such as Dunlin respond to the presence of predators by flocking (Buchanan 1980, Caraco et al. 1980, Myers 1980). Flocking enhances predator avoidance either through confusion or dilution effects (Creswell 1994, Hamilton 1971, Kenward 1978) or an earlier detection of the predator resulting from shared vigilance. ("many eyes" hypothesis, Pulliam 1973). Ekman (1987) and Suhonen (1993) found larger flocks in high-predation risk situations compared to low-risk situations. On the other hand, birds spend more time scanning for predators when predation risk increases (Caraco et al. 1980, Ekman 1987). I predicted that in rice fields (high-risk habitat), Dunlin flocks would be larger than in littoral habitats (low-risk habitat) and that they will spend more time scanning in rice fields than in littoral areas.

METHODS

The study was conducted at the Ebro Delta Natural Park (northeastern Spain; 40°43′N, 00°44′E), one of the main wintering areas for Dunlin in the Mediterranean with around 10,000 individuals (Barbosa 1992, Grimmet and Jones 1988). Observations were made November–April in 1990–1991 and 1991–1992. The area consisted of rice fields (15,000 ha), market garden (9,500 ha), and natural wetlands (beaches, salt marshes, lagoons) (7,500 ha). The area potentially suitable for shorebirds was 16,000 ha (Martínez-Vilalta 1985).

In this area there are five raptor species present (*Circus aeroginosus* [3.21 individuals/km^2], *Circus cyaneus* [0.28], *Buteo buteo* [1.21], *Falco tinnunculus* [1.10]) and *Falco columbarius* ([0.07]; Tombal and Tombal 1988). Raptor species such as these may have considerable impact on survival rates of wintering shorebirds (Creswell and Whitfield 1994, Page and Whitacre 1975).

Scanning behavior was recorded using the focal observation method (Altmann 1974). Focal birds were randomly chosen during regular surveys of the study area, and their behavior was tape-recorded during a 2-min period, on average (range = 1–3.5 min). All observations were made during daylight with 8×30 binoculars or a 40×60 spotting scope. To avoid problems of pseudoreplication (Hulbert 1984), I attempted to sample individuals only once. Because birds were not color-marked, I sampled birds in a way to maximize the chance of observing different individuals (i.e., in a flock of about 100 individuals, I sampled 5–10 birds from the far side, 5–10 birds from the near side, 5–10 birds from the left side, and 5–10 individuals from the right side of the flock). Each bird sampled was at least was 20 m from the previous bird sampled. This procedure maximized the chance that different individuals were sampled

TABLE 1. Scanning and flocking behavior of Dunlins in two habitats at the Ebro Delta, Spain, 1991–1992.

	Vigilance rate (scan/min)		Time spent vigilant (%)		Mean scan duration (s)		Flock size	
Habitats	x̄	SE	x̄	SE	x̄	SE	x̄	SE
Rice fields	1.76	0.25	4.20	1.17	0.96	0.14	293.92	23.51
Littoral	1.03	0.19	1.74	0.44	0.42	0.09	189.44	31.52

(Barbosa 1995, 1996). Vigilance rate (number of scans per minute foraging), vigilance time (percentage of time spent scanning while feeding), and mean scan duration were recorded as variables characterizing scanning behavior (Barbosa 1995). A scan was defined as raising the head from the head-down foraging position to a position with the bill line above the horizontal (Barbosa 1995). All birds were sampled while actively foraging, this avoided bias due to differences in scanning behavior related to another behavior such as resting or preening. I considered a flock as all birds (con- and hetero-specific) within 10 m of the nearest neighbor.

Scanning behavior is affected by flock size, with individual levels of vigilance decreasing as the number of individuals increases (e.g., Abramson 1979). However, I did not find any significant relationship between scanning variables and flock size (scan rate $r = 0.08$ $P > 0.05$; mean scan duration $r = 0.05$ $P > 0.05$; time spent vigilant $r = 0.06$ $P > 0.05$). Therefore, data were not corrected for flock size in subsequent analyses.

Analysis of variance (ANOVA) was used to analyze the differences between scanning and flocking variables with differential predation risk. Percentages were arcsin-transformed prior to analysis.

RESULTS

I observed 77 individuals in littoral habitats and 28 in rice fields. Scanning and flocking behavior differed between habitats. Mean scan duration was significantly longer in rice fields (high-risk habitat) than in littoral (low-risk habitat) ($F_{1,104} = 8.97$, $P < 0.01$; Table 1). Dunlins spent more time vigilant in rice fields than in littoral ($F_{1,104} = 5.78$, $P < 0.01$; Table 1). Vigilance rate also showed significant differences between habitats ($F_{1,104} = 4.00$, $P < 0.05$; Table 1). Flocks were larger in high-risk habitats than in low-risk habitats ($F_{1,104} = 3.70$, $P = 0.05$; Table 1).

DISCUSSION

Recent studies focus on predator abundance or presence as the prime determinant of risk in habitat use trade-offs. Caldwell (1986) reported that foraging herons switch from areas in which predatory attacks are common to those where predators are rare, even though the safe areas are less energetically profitable. Grubb and Greenwald (1982) found that patch selection in House Sparrows reflects a predation-energy trade-off influenced by the distance to protective cover. This is also true for Willow Tits (Hogstad 1988). At Ebro Delta, more profitable areas (littoral) have space constraints and birds must use less-profitable areas (rice fields) to minimize the risk of starvation in winter (Barbosa 1996), although the latter habitat has a high predation risk. During winter at Ebro Delta predation pressure by raptors (*Circus aeroginosus, Circus cyaneus, Buteo buteo* and *Falco tinnunculus*) is higher in rice field than in litoral (Tombal and Tombal 1988). Therefore, to compensate for possible costs derived from the use of rice fields, Dunlins change their behavior when feeding in littoral areas.

Mean flock size, mean scan duration, vigilance rate and time spent scanning are higher in rice field than in litoral. Flocking probably enhances predator avoidance as individuals may benefit from an earlier detection of the predator by sharing vigilance (Pulliam 1973) and from a confusion or dilution effect (Hamilton 1971, Kenward 1978). Predation seems to be a major selective pressure influencing flocking behavior in foraging winter shorebirds (Abramson 1979, Page and Whitacre 1971, Stinson 1980), in terms of a decreased proportion of time that each individual spends in antipredator vigilance (Glück 1987, Metcalfe 1989, Redpath 1988). Several authors (Caraco et al. 1990, Carrascal and Moreno 1992, Ekman 1987, Suhonen 1993) found larger flocks and birds spending more time vigilant at high predation risk than at low predation risk.

On the other hand, lengthening scan duration achieves a higher level of vigilance with lower frequency of changes between vigilant and non-vigilant states, thus saving the time and energy necessary to rise and lower their heads (Studd et al. 1983) and without interrupting the search for hidden prey difficult to capture (Carrascal et al. 1990). Short scans do not allow a large visual field to be scanned whereas long scans would provide complete information (Desportes et al. 1993). Mean scan duration also has been related to differences in the complexity of the environment that could provide protective cover (Carrascal and Moreno 1992, Metcalfe 1984). However, in my study area, habitats have similar complexity (Barbosa 1994). This shows that predation pressure seems to be more important that habitat complexity in modifying scan duration of Dunlins at Ebro Delta. On the other hand, predator detection in the larger surrounding area, as inhabited by Dunlins, should require a longer time for a correct evaluation of the risk (Carrascal and Moreno 1992).

Behavioral changes displayed by Dunlin between habitats with different predation risk agree with previous studies. By increasing variables related to scanning and flocking behavior, birds probably increase efficiency in predator avoidance and likely compensate the costs derived for the use of high-predation-risk habitat under starvation risk as theory predicts.

ACKNOWLEDGMENTS

This study has been carried out with the collaboration of the Agriculture and Fish Department of the Catalonian Generalitat and the Natural Park of Delta del Ebro. Financial support was provided by a CSIC-CAM grant and partly by Caja Madrid. Laura provided considerable assistance.

LITERATURE CITED

ABRAMSON, M. 1979. Vigilance as a factor influencing flock formation among curlews *Numenius arquata.* Ibis 121:213–216.

ALATALO, R. V. 1982. Evidence for interspecific competition among European tits *Parus* spp.: a review. Annales Zoologici Fennici 19:309–317.

ALTMANN, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49:227–267.

ANDERSON, P. K. 1986. Foraging range in mice and voles: the role of risk. Can. J. Zool. 64: 2645–2653.

BARBOSA, A. 1992. Areas importantes para limícolas en España. *In* Amigos de la Tierra, eds. Aves Limícolas. Anuario Ornitológico. Miraguano, Madrid.

———. 1994. Estudio ecomorfológico de las aves limícolas (Aves: Charadrii): modificaciones adaptativas relacionadas con la búsqueda del alimento. Ph.D. Thesis, Universidad Complutense, Madrid, Spain.

———. 1995. Foraging strategies and their influence on scanning and flocking behaviour of waders. J. Avian Biol. 26:182–186.

———. 1996. Foraging habitat use in a Mediterranean estuarie by Dunlin, *Calidris alpina.* Journal of Coastal Research 12:996–999.

BUCHANAN, J. B., C. T. SCHICK, L. A. BRENNAN, AND S. G. HERMAN. 1988. Merlin predation on wintering dunlins: huntins success and dunlins escape tactics. Wilson Bull. 100:108–118.

CALDWELL, G. S. 1986. Predation as a selective force on foraging herons: effects of plumage color and flocking. Auk 103:494–505.

CARACO, T. 1979. Time budgeting and group size: a test of theory. Ecology 60:618–627.

———, S. MARTINDALE, AND H. R. PULLIAM. 1980. Avian flocking in the presence of a predator. Nature 285:400–401.

CARRASCAL, L. M., J. C. ALONSO AND J. A. ALONSO. 1990. Aggregation size and foraging behaviour of White Storks *Ciconia ciconia* during the breeding season. Ardea 78:399–404.

———, AND E. MORENO. 1992. Scanning behaviour and spatial niche. J. Orn. 133:73–77.

CRESWELL, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus.* Anim. Behav. 47:433–442.

———, AND D. P. WHITFIELD. 1994. The effects of raptor predation on wintering wader populations at the Tyninghame estuary, southeast Scotland. Ibis 136:223–232.

DESPORTES, J. P., N. B. METCALFE, J. W. POPP, R. M. MEYER, A. GALLO, AND F. CEZILLY. 1993. Relationships between scan and interscan durations in three avian species. Can. J. Zool. 71:1466–1469.

EKMAN, J. 1987. Exposure and time use in willow tit flocks: the cost of subordination. Anim. Behav. 35:508–514.

FERGUSON, S. H., A. T. BERGERUD, AND R. FERGUSON. 1988. Predation risk and habitat selection in the persistence of a remmant caribou population. Oecologia 76:236–245.

GLÜCK, E. 1987. An experimental study of feeding vigilance and predator avoidance in a single bird. Oecologia 71:268–272.

GRIMMET, R., AND T. JONES. 1989. Important bird areas in Europe. ICBP Technical Publications.

GRUBB, T. C. AND L. GREENWALD. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation riks and energy cost. Anim. Behav. 30:637–640.

HAMILTON, W. D. 1971. Geometry for selfish herd. J. Theor. Biol. 31:295–311.

HOGSTAD, O. 1988. Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flocks. Ibis 130:45–56.

HULBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187–211.

KENWARD, R. E. 1978. Hawks and doves: factors affecting success and selection in goshawks and wood-pigeons. J. Anim. Ecol. 47:449–460.

LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68:619–640.

MARTINEZ-VILALTA, A. 1985. Descripción de la comunidad de limícolas invernante del Delta del Ebro. Doñana Acta Vertebrata. 12:211–229.

METCALFE, N. B. 1984. The effects of habitat on the vigilance of shorebirds: is visibility important? Anim. Behav. 32:981–985.

———. 1989. Flocking preferences in relation to vigilance benefits and agression costs in mixed-species shorebird flocks. Oikos 56:91–98.

MYERS, J. P. 1980. Territoriality and flocking by Buff-breasted Sandpipers: variations in non-breeding dispersion. Condor 82:241–250.

PAGE, G., AND D. F. WHITACRE. 1975. Raptor predation on wintering shorebirds. Condor 77: 73–83.

PULLIAM, H. R. 1973. On the advantages of flocking. J. Theor. Biol. 38:419–422.

REDPATH, S. 1988. Vigilance levels in preening Dunlin *Calidris alpina*. Ibis 130:555–557.

STINSON, C. H. 1980. Flocking and predator avoidance: models of flocking and observations on the spatial dispersion of foraging wintering waders (Charadrii). Oikos 34:35–43.

STUDD, M., R. D. MONTGOMERIE, AND R. J. ROBERTSON. 1983. Group size and predator surveillance in foraging house sparrows (*Passer domesticus*) Can. J. Zool. 61:226–231.

SUHONEN, J. 1993. Predation risk influences the use of foraging sites by tits. Ecology 74: 1197–1203.

TOMBAL, C., AND J. C. TOMBAL. 1988. Les rapaces diurnes dans le Delta de l'Ebre au mois de decembre. Bulletin Parc Natural Delta de l'Ebre 3:28–35.

WEISSBURG, M. 1986. Risky business: on the ecological relevance of risk-sensitivity foraging. Oikos 46:261–262.

Received 8 Jun. 1996; accepted 19 Dec. 1996.