EFFECTS OF RAPTORS ON THE ACTIVITY OF SANDGROUSE

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ABSTRACT.—Raptors accounted for 55% of the disturbance incurred by two species of sandgrouse (*Pterocles alchata* and *P. orientalis*) in breeding habitat in La Mancha, Spain, during spring and summer. The main species of raptors were the golden eagle (*Aquila chrysaetos*) in spring and Montagu's harrier (*Circus pygargus*) in summer. During the breeding season, Montagu's harriers carried out the majority of their foraging at those times of day when male sandgrouse collected water for their chicks. This presumably enabled the harriers to locate chicks more easily. Sandgrouse lost no more than 0.5 hr of feeding time per day as a result of disturbance by raptors, and yet were still able to rest for at least 3 hr a day at times when they could have been feeding. Predators as a whole were probably the major factor responsible for the different dispersion patterns adopted by sandgrouse at different times of year.

KEY WORDS: *golden eagle; Montagu's harrier;* Pterocles alchata; Pterocles orientalis; *raptor disturbance; sandgrouse; vigilance.*

RESUMEN.—Aves rapaces fueron responsables por 55% de las perturbaciones sufridas por dos especies de gangas (*Pterocles alchata* and *P. orientalis*) en sus areas de reproducción en la Mancha, España, durante la primavera y el verano. Las especies de aves de rapiña más prominentes fueron el águila real (*Aquila chrysaetos*) en la primavera y el aguilucho cenizo (*Circus pygargus*) en el verano. Durante la estación de reproducción los aguiluchos cenizos llevaron a cabo la mayoría de su forrajeo en las horas del día en que las gangas machos estaban recogiendo agua para sus pollos. Esto supuestamente les permitió a los aguiluchos localizar los pollos más facilmente. Las gangas perdieron no más de media hora del tiempo de alimentación diario debido a las perturbaciones por aves de rapiña sin embargo estuvieron inactivos por lo menos durante 3 horas al día cuando hubieran podido estar alimentando. Las aves de rapiña en general fueron probablemente el factor más importante en determinar los distintos partrones de dispersión de las gangas en distintas épocas del año.

[Traducción Autores]

Raptors can exert a significant influence on the flocking behavior of birds, both in the short term and the long term. In response to attacks by sparrowhawks (*Accipiter nisus*), redshanks (*Tringa totanus*) deserted their winter feeding territories for up to an hour and formed flocks, while turnstones (*Arenaria interpres*) reduced their individual spacing from three bird lengths to one bird length (Whitfield 1988). Myers (1984) found that winter feeding territories were abandoned by sanderlings (*Calidris alba*) in years when merlins (*Falco columbarius*) were more abundant. These studies focused on the influence of raptors on the flocking and vigilance of potential prey (see also Metcalfe 1989). The amount of time for which target organisms are prevented from carrying out other activities has seldom been measured. In one early study, Morse (1973) found that spar-

rowhawks attacked particular tit (*Parus* spp.) flocks about once per day on average, and disturbed the birds for only about 2 min. Longer disturbances can be inferred from detailed studies of merlins and sparrowhawks attacking wintering waders (Page and Whitacre 1975, Boyce 1985, Cresswell and Whitfield 1994), though no actual estimates are available in these cases.

In order to derive estimates of the total time lost by pin-tailed sandgrouse (*Pterocles alchata*) and black-bellied sandgrouse (*P. orientalis*) as a result of disturbance by raptors, we recorded the amount of time the birds spend being vigilant, the number of incidents of disturbance and the factors responsible. This was done as part of the compilation of time and energy budgets for these two species of sandgrouse in Spain.

STUDY AREA AND METHODS

Observations were made in semi-arid farmland in the province of La Mancha, Spain, in spring (29 March to 21 April) and summer (22 July to 10 August) 1986. Sandgrouse occurred in flocks during the spring, comprising on average 26 (SD = 23, N = 31) individuals in pin-tailed sandgrouse, with a maximum flock size of 75. Most daytime flocks of black-bellied sandgrouse contained 2–7 birds, though slightly larger groups (maximum 28) roosted together overnight. In summer, both species occurred in scattered family groups. When compiling time budgets, we scan-sampled bird activity at 1 min intervals. In both seasons, the day was divided into 10 equal time periods. These time periods were longer in summer (92 min) than in spring (82 min). The field area and study methods are described elsewhere (Hinsley 1994, Hinsley and Ferns 1994). A total of over 46 000 bird observations were made, involving on average 29 pin-tailed sandgrouse and 6 black-bellied sandgrouse each day in spring, and family groups of 2–5 pin-tailed sandgrouse in summer (at least two different families were watched each day, and over 40 families were studied in total). Every potential predator that was observed close enough to the focal birds to disturb them was recorded. If the same source of disturbance caused more than one group of birds to react, this was treated as a single incident, even if the events occurred a considerable time apart (actual maximum = 7 min).

The observations in the spring were undertaken at a range of 300–1000 m (typically 700 m) to avoid disturbing the birds, and it was not possible to distinguish gender at this time of year. Observations in the summer were undertaken at a range of 200–800 m (typically 400 m). In the summer, groups split up into family parties in which males, females and juveniles (1–2-mon-old at the time of the observations) were distinguishable.

To estimate the amount of time that sandgrouse spent being vigilant when disturbed, we performed stepwise regression on the percentage of time spent being vigilant (arcsine transformed) in each of the 10 daily time periods against the number of records of disturbance caused by all factors that we were able to identify. These were divided into five categories comprising the numbers of the most common raptors in each season (golden eagle [*Aquila chrysaetos*] in spring, Montagu's harrier [*Circus pygargus*] in summer); other raptors; other birds (mainly red-legged partridges [*Alectoris rufa*] and great grey shrikes [*Lanius excubitor*]); mammals (rabbits, sheep and dogs); and humans (including noises caused by human activities). This method of measuring the affect of disturbance has the advantage of taking into account losses of feeding time through increased alertness even when this lasted for some time after the disturbance ended.

RESULTS

In the absence of disturbance, sandgrouse vigilance was typically restricted to short bouts with the head up. The duration of these bouts was longest in male pin-tailed sandgrouse accompanying chicks ($\bar{x}$ = 6.5 sec, SD = 3.9, N = 47). When disturbed,

Table 1.   Number of raptors observed while compiling sandgrouse time budgets.

RAPTOR SPECIES	NUMBER OF SIGHTINGS OF EACH RAPTOR	
	SPRING N = 23 da	SUMMER N = 20 da
Black kite (*Milvus migrans*)	4	
Red kite (*M. milvus*)	6	
Montagu's harrier (*Circus pygargus*)	1	23
Common buzzard (*Buteo buteo*)	3	4
Imperial eagle (*Aquila heliaca*)	2	
Golden eagle (*A. chrysaetos*)	11	
Booted eagle (*Hieraaetus pennatus*)		1
Common kestrel (*Falco tinnunculus*)		1
Peregrine falcon (*Falco peregrinus*)	1	2
Little owl (*Athene noctua*)	1	

sandgrouse adopted alert upright postures or crouched close to the ground (these behaviors were also recorded as vigilance).

The most common identified source of disturbance was raptors. During a total of 43 d of observations, the number of disturbances due to raptors was 60. A further 49 disturbances were attributed to other causes. The species of raptors involved (Table 1) differed significantly between spring and summer, though the number of incidents was very similar. The most important species in spring was the golden eagle. The most important species in summer was Montagu's harrier (golden eagles were absent from the area during the summer). Because the same individual raptor may have caused disturbance on more than one day, there may have been some unavoidable pseudoreplication. However, the proportion of disturbances caused by the most abundant raptor (compared with all other birds) in the two seasons was significantly different (Fisher's exact test, P < 0.005). A greater diversity of raptors was thus responsible for disturbance during the spring (Table 1). Red kites (*Milvus migrans*) and black kites (*M. milvus*) were recorded in spring but not summer, both being migrants in the area. A flock of 106 black kites that passed over on migration on the evening of 3 August was not included since it caused no disturbance.

Golden eagles were observed circling quite high (about 30–50 m) over the fields and hill slopes, and
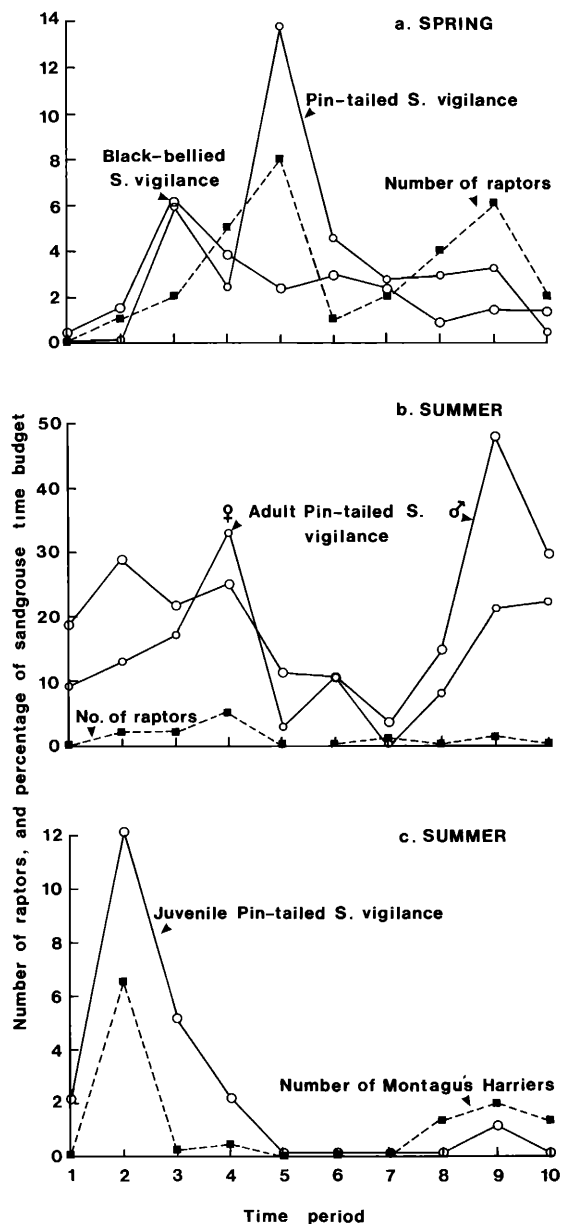
Figure 1.   Selected raptor activity (numbers) and sandgrouse vigilance (percentage of time budget) throughout the daylight period. The total number of raptors is shown in spring (a), the total number of raptors other than Montagu's harriers (b), and number of Montagu's harriers in summer (c).

also perched on vantage points overlooking the fields. Both golden eagles and red kites regularly take birds the size of adult sandgrouse (Cramp and Simmons 1979). In spring, a juvenile imperial eagle (*Aquila heliaca*) took a taxidermic mount of a sandgrouse (used to measure operative temperature) from the ground and was only prevented from flying off with it by the attached data-logger. Montagu's harriers and red kites quartered the fields at a height of only a few meters, and occasionally circled at a greater elevation. In summer, Montagu's harriers were observed attacking young sandgrouse, but not adults. The young of ground-nesting birds form a considerable part of this harrier's diet during the summer months (Cramp and Simmons 1979).

Vigilance of adult sandgrouse in each time period (Fig. 1) peaked during the middle of the day in spring, and during the morning and evening in summer. The gap between the summer peaks coincided with a period of reduced activity of both raptors and sandgrouse in the middle of the day, induced by high temperature. The vigilance of juvenile sandgrouse reached a peak earlier in the morning than that of adults. Adult males spent more time being vigilant in summer than in spring (19% of daylight hours compared with 3%), presumably because of the vulnerability of their offspring during the former period. This difference was statistically significant (Kruskal-Wallis test, $H = 11.3$, $P = 0.001$.

While male and female vigilance in the 10 daily time periods were correlated significantly during summer ($r = 0.69$, $P < 0.02$, $N = 10$), juvenile vigilance was not correlated with that of either parent ($r = 0.46$ with males and $r = 0.12$ with females, $P > 0.10$ in both cases). This is largely because juveniles spent most of the day feeding or resting, relying on their parents to act as sentinels (especially their fathers). They showed most alertness when he was away collecting water for them during the morning and when he returned. Juveniles were less sensitive to disturbance by Montagu's harriers in the evenings (Fig. 1), probably because the latter spent most of their time hunting rabbits during this period of the day.

Sandgrouse responded to raptors differently in spring and summer, and this reflected the different dispersion pattern they adopted in the breeding season because of the vulnerability of their young (Lima and Dill 1990). In neither spring nor summer did the sandgrouse form denser groups when disturbed; if anything the flocks tended to split up. In spring,

they merely flew to another of the several fields in which they normally foraged during the course of the day. In summer, the first response of both adults and young to the presence of a raptor was to crouch and freeze. If a family group was located by a raptor, the adults usually mobbed it before flying off, while the young ran or flew into the nearest dense vegetation. Consequently, their activity was affected mainly by a direct loss of time available for feeding, preening, drinking and other activities. We saw three direct attacks by Montagu's harriers on juvenile sandgrouse, all unsuccessful, and adults with young mobbed Montagu's harriers on four additional occasions. Male vigilance showed no significant correlation with disturbance factors, mainly because they spent such a high proportion of the time alert, even in the absence of any obvious disturbance (19% of daylight hours spent alert, compared with 12% in females).

Since disturbance often caused sandgrouse to fly in spring, there was significantly more sandgrouse alertness in time periods in which the birds spent more time flying ($r = 0.80$, $P < 0.01$, $N = 10$ in all cases). In summer, reduced levels of alertness in both sexes of pin-tailed sandgrouse were associated with periods of resting (males, $r = -0.68$, $P < 0.05$; females, $r = -0.67$, $P < 0.05$). Differences in flock sizes were not significant in different time periods, nor was alertness significantly correlated with flock size in either species. Therefore, alertness within seasons was not significantly correlated with any variable that might have confounded its correlation with disturbance, including flock size or distance to cover (Elgar 1989).

Stepwise regression analysis indicated that a high proportion of the time spent being vigilant was accounted for by the observed sources of disturbance, despite the small sample size ($N = 10$ in all cases). In spring, 48% of the variation in pin-tailed sandgrouse vigilance between time periods was accounted for by the overall number of raptors recorded ($t = 3.2$, $P < 0.02$) and 20% by human disturbances ($t = 2.4$, $P = 0.05$). In summer, 46% of female vigilance was accounted for by raptors other than Montagu's harriers ($t = 2.5$, $P < 0.05$) and 25% by mammals ($t = 2.5$, $P < 0.05$). Also in summer, 68% of juvenile vigilance was accounted for by the number of Montagu's harriers ($t = 4.1$, $P = 0.003$). Fifty-seven percent of black-bellied sandgrouse vigilance in spring was accounted for by disturbance caused by dogs, sheep and rabbits ($t = 5.6$, $P = 0.001$), and 19% by

that caused by humans ($t = 4.8$, $P = 0.003$). The larger size of this species apparently made it less vulnerable to disturbance by most raptors.

DISCUSSION

While the spring flocks of sandgrouse may have been reasonably easy for golden eagles and other raptors to locate, they did not provide a particularly easy target as indicated by the rarity of the attacks we witnessed. Young sandgrouse during the breeding season were much more vulnerable, though they must have been more difficult to locate in the well-dispersed family groups. It is thus not surprising that Montagu's harriers concentrated most of their foraging activity in the period when male sandgrouse returned with water from the waterholes, since this provided them with a potential clue to the whereabouts of young. Such predation pressure may have led in turn (c.f. Lima and Dill 1990) to a wider spread of watering times amongst males in this area, including evening watering. The two species of sandgrouse we observed tended to forage in different types of habitat (Hinsley 1994), but we do not believe that this choice was influenced by raptor activity. The pin-tailed sandgrouse was the more vulnerable species, but it foraged in open fields where it was more visible than on the hill slopes favored by black-bellied sandgrouse. As suggested by Lima and Dill (1990), vigilance costs were higher during the breeding season. Adults with young were also prepared to run greater risks by mobbing raptors during the summer.

Predation of young sandgrouse probably represents a major source of mortality (Maclean 1985). However, young are likely to be even more vulnerable to raptors at water holes (Cade 1965) and this may explain why males continued to carry water to them even after they had become capable of flying to water holes for themselves. Raptors recorded attacking or consuming sandgrouse in other areas include pallid harrier (*Circus macrourus*), golden eagle, greater kestrel (*Falco rupicoloides*), sooty falcon (*F. concolor*), lanner falcon (*F. biarmicus*) and Barbary falcon (*F. pelegranoides*) (Ali and Ripley 1983, Cramp 1985, Urban et al. 1986).

The amount of time males with young spent being vigilant (19% of daylight hours) was much less than that of male barnacle geese (*Branta leucopsis*) escorting their broods (48%) (Forsland 1993). In both species, the males devoted more time to vigilance

than the females. Walters (1990) found no difference in the response of long-toed lapwings (*Vanellus crassirostris*) and blacksmith plovers (*V. armatus*) according to whether or not they had young, but they did respond more strongly to harriers than to eagles.

The intensity of predatory disturbance at our study site was relatively low compared with some others. For example, at Bolinas Lagoon in California, a single merlin mounted about 19 attacks per day on shorebirds (Page and Whitacre 1975). However, the 5000 potential prey in this area were divided into groups of at most several hundred, and therefore the disturbance incurred per bird was much lower. Calvo (1993) recorded more than 10 disturbances per day (an order of magnitude more than that caused by raptors at our site) at breeding colonies of collared pratincoles (*Glareola pratincola*) in southwest Spain. Black kites and common kestrels (*Falco tinnunculus*) were responsible for most pratincole disturbance, though Montagu's harriers were also seen taking chicks.

Most of the time sandgrouse spent being vigilant as a result of the activities of raptors, humans, and other mammals was time they would otherwise have spent feeding. In the middle of the day, when birds rested in the shade of shrubs, alertness and disturbance levels were relatively low and the small amount of disturbance that did occur then was usually caused by red-legged partridges.

None of the results described here suggest that disturbance by raptors presented sandgrouse with any difficulty in meeting their daily energy requirements. The time of the year when the highest proportion of the day was occupied by foraging was the spring, and even then black-bellied sandgrouse were still able to devote over 3 hr, and pin-tailed sandgrouse over 4 hr, to resting at times when they could presumably have been feeding. The above regressions enable us to estimate that raptors in spring caused pin-tailed sandgrouse to lose about 24 min of foraging time per day. Mammals caused black-bellied sandgrouse to lose 10 min per day at the same time of year. In summer, Montagu's harriers caused juvenile pin-tailed sandgrouse to lose 9 min per day. Other raptors caused adult females to lose about 25 min. Raptors may be the largest single source of disturbance, but man and other mammals also caused some, even in this thinly populated area. Predators as a whole were probably a major factor responsible for the different dispersion patterns adopted by pre-breeding and breeding sandgrouse.

LITERATURE CITED

ALI, S. AND S.D. RIPLEY. 1983. Handbook of the birds of India and Pakistan. Oxford Univ. Press, Oxford, U.K.

BOYCE, D.A. 1985. Merlins and the behavior of wintering shorebirds. *Raptor Res.* 19:94–96.

CADE, T.J. 1965. Relations between raptors and columbiform birds at a desert water hole. *Wilson Bull.* 77: 340–345.

CALVO, B. 1993. Influences of agricultural land-use and habitat modification on the breeding biology and conservation of collared pratincoles *Glareola pratincola* in SW Spain. Ph.D. dissertation, Univ. Glasgow, U.K.

CRAMP, S. [ED.]. 1985. The birds of the western Palearctic. Vol. 4. Oxford Univ. Press, Oxford, U.K.

——— AND K.E.L. SIMMONS. [EDS.]. 1979. The birds of the western Palearctic. Vol. 2. Oxford Univ. Press, Oxford, U.K.

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

ELGAR, M.A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev. Camb. Philos. Soc.* 64:13–33.

FORSLAND, P. 1993. Vigilance in relation to brood size and predator abundance in the barnacle goose, *Branta leucopsis. Anim. Behav.* 45:965–973.

HINSLEY, S.A. 1994. Daily time budgets and activity patterns of sandgrouse (Pteroclididae) in contrasting arid habitats in Spain and Israel. *J. Arid Environ.* 26: 373–382.

——— AND P.N. FERNS. 1994. Time and energy budgets of breeding males and females in sandgrouse *Pterocles* species. *Ibis* 136:261–270.

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.

MACLEAN, G.L. 1985. Sandgrouse: models of adaptive compromise. *S. Afr. J. Wildl. Res.* 15:1–6.

METCALFE, N.B. 1989. Flocking preferences in relation to vigilance benefits and aggression costs in mixed-species shorebird flocks. *Oikos* 56:91–98.

MORSE, D.H. 1973. Interactions between tit flocks and sparrowhawks *Accipiter nisus. Ibis* 115:591–593.

MYERS, J.P. 1984. Spacing behavior of nonbreeding shorebirds. Pages 271–321 *in* J. Burger and B.L. Olla

[EDS.], Behavior of marine animals. Vol. 6. Shorebirds. Migration and foraging. Plenum Press, NY U.S.A.

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

URBAN, E.K., C.H. FRY AND C.S. KEITH. [EDS.]. 1986. The birds of Africa. Vol. 2. Academic Press, London, U.K.

WALTERS, J.R. 1990. Anti-predatory behavior of lap-

wings: field evidence of discriminative abilities. *Wilson Bull.* 102:49–70.

WHITFIELD, D.P. 1988. Sparrowhawks *Accipiter nisus* affect the spacing behavior of wintering turnstone *Arenaria interpres* and redshank *Tringa totanus. Ibis* 130. 284–287.