



DIURNAL STUDIES DO NOT PREDICT NOCTURNAL HABITAT CHOICE AND SITE SELECTION OF EUROPEAN GOLDEN-PLOVERS (*PLUVIALIS APRICARIA*) AND NORTHERN LAPWINGS (*VANELLUS VANELLUS*)

SIMON GILLINGS,^{1,3} ROBERT J. FULLER,¹ AND WILLIAM J. SUTHERLAND²

¹British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, United Kingdom; and

²Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, United Kingdom

ABSTRACT.—Many species, including shorebirds, feed during both day and night, yet little is known about how this affects behavior and habitat preferences. European Golden-Plovers (*Pluvialis apricaria*) and Northern Lapwings (*Vanellus vanellus*) feeding on arable farmland were more widely dispersed at night: nocturnal flocks were smaller, typically monospecific, and occurred in many more fields than diurnal mixed-species flocks. Diurnal numbers of European Golden-Plovers could not be used to predict nocturnal numbers; this indicates that ranging behavior differed between day and night. For both species, nocturnal feeding was recorded on almost all nights, irrespective of moon phase. Northern Lapwing nocturnal feeding activity decreased with increasing cloud cover and decreasing ground temperature, but no clear relationships were detected between European Golden-Plovers' nocturnal feeding activity and environmental variables. Habitat selection differed between day and night, and between species at night. Diurnal studies of habitat choice and site selection may misrepresent the full requirements of such species. Received 20 April 2004, accepted 8 April 2005.

Key words: European Golden-Plover, habitat selection, nocturnal, Northern Lapwing, *Pluvialis apricaria*, *Vanellus vanellus*.

Los Estudios Diurnos no Predicen la Preferencia Nocturna de Hábitat ni la Selección Nocturna de Sitio en *Pluvialis apricaria* y *Vanellus vanellus*

RESUMEN.—Muchas especies, incluyendo especies de aves costeras, se alimentan tanto durante el día como durante la noche. Sin embargo, se sabe muy poco si esto puede afectar el comportamiento y las preferencias de hábitat de estas especies. Los individuos de *Pluvialis apricaria* y *Vanellus vanellus* que se alimentan en terrenos agrícolas arables presentaron una distribución más amplia durante la noche: las bandadas nocturnas fueron más pequeñas, fueron generalmente monoespecíficas y se presentaron en muchos más campos que las bandadas mixtas diurnas. Los números diurnos de *P. apricaria* no pudieron ser usados para predecir los números nocturnos, lo que indica que el comportamiento de distribución difiere entre el día y la noche. Para las dos especies, se registró alimentación nocturna en casi todas las noches, independientemente de la fase lunar. La actividad de alimentación nocturna de *V. vanellus* disminuyó con el aumento de la cobertura de nubes y con la disminución de la temperatura del suelo, pero no se detectaron relaciones claras entre la actividad de alimentación nocturna de *P. apricaria* y las variables ambientales. La selección de hábitat difirió entre el día y la noche y entre especies durante la noche. Los estudios diurnos sobre preferencia de hábitat y selección de sitio pueden tergiversar la totalidad de los requerimientos de estas especies.

³E-mail: simon.gillings@bto.org

ENERGY INTAKE DURING daylight hours alone is insufficient to balance energy budgets in many shorebird species (e.g. Morrier and McNeil 1991, Sitters 2000). This is particularly true of species that feed in intertidal environments where prey are inaccessible for long periods, or those that winter in temperate regions where short day length restricts feeding opportunities. In such cases, nocturnal feeding is assumed to occur, and there is now a growing body of literature on the degree of nocturnal feeding, its environmental correlates, and its profitability (McNeil et al. 1992, Thibault and McNeil 1994, Hötter 1999, Smith et al. 1999, Sitters 2000, Sitters et al. 2001). There have been few studies of nocturnal behavior in terrestrial (as opposed to intertidal) shorebirds, with the exception of the woodcocks (*Scolopax* spp.; e.g. Berdeen and Kremetz 1998). The nocturnal behaviors of European Golden-Plovers (*Pluvialis apricaria*; hereafter "golden-plovers") and Northern Lapwings (*Vanellus vanellus*; hereafter "lapwings") have not been considered in detail.

Golden-plovers and lapwings winter on agricultural fields throughout temperate northwestern Europe (Cramp and Simmons 1983). Though they are not restricted by tidal cycles and can potentially feed throughout daylight hours, they rarely do so, and several studies suggest strong lunar periodicity in diurnal feeding activity. Spencer (1953) noted that lapwings were often inactive during the day on and around the full moon. Milsom (1984) also found that day-roosting of lapwings increased around the full moon, but he showed that there was never complete cessation of diurnal feeding. Similar activity patterns were found for both species by Kirby (1997). In the present six-year study, the proportion of both lapwings and golden-plovers feeding by day was significantly related to moon phase, as expected, though temperature appeared to have an overriding effect by increasing diurnal feeding during cold weather (Gillings 2003). Klomp and van der Starre (1956) found that, in both autumn and spring, the number of lapwings caught at the Reeuwijk ringing station (The Netherlands) increased following moonlit nights. Similarly, Jukema et al. (2002) found that diurnal catches were typically twice as large during the full moon as during the new moon. Why capture rates should differ in this way is unclear, but the difference suggests that moon phase can have a strong effect on golden-plover and lapwing activity.

Following these daytime observations, it was generally assumed that golden-plovers and lapwings fed at night only when the moon was full. Nocturnal observations by Milsom et al. (1990) supported this assumption. However, in the study by Gillings (2003), golden-plovers and lapwings rarely fed throughout the entire period of daylight hours, even during new-moon periods, and observed diurnal intake rates were insufficient to meet daily energy requirements. This indicates that nocturnal feeding must occur, to some degree, throughout the lunar cycle. Therefore, one aim of the present study is to ascertain (1) the degree to which nocturnal feeding occurs in golden-plovers and lapwings and (2) what factors affect its prevalence.

Differences in predation risk and growth rates explain day–night habitat shifts in fish species (Greenwood and Metcalfe 1998, Greenberg and Giller 2001), and similar day–night differences in environmental and biotic factors should influence shorebird behavior. The range of potential predators may differ, as may the mechanisms by which they are detected. During the day, flocking may reduce an individual's predation risk (Krause and Ruxton 2002), but at night it may not enhance predator detection (and may even attract predators), and other negative effects of flocking (e.g. passive interference) may become costly. Patches may differ in their predator populations between day and night. Such processes may explain why Red Knot (*Calidris canutus*) wintering in South America switched from feeding in dense flocks on inshore *restingas* (rock platforms) during the day to feeding in loose flocks on offshore mudflats at night (Sitters et al. 2001). Similar day–night habitat shifts have been noted for Dunlin (*C. alpina*) on temperate estuaries (Mouritsen 1994) and Wilson's Plovers (*Charadrius wilsonia*) on tropical lagoons (Thibault and McNeil 1994). Also, switches in habitat may be influenced by the prey available at different sites and visual constraints on foraging modes. Many species locate prey using visual cues by day but are forced to switch to tactile foraging because of poorer visual capability at night (Rojas de Azuaje et al. 1993, Rojas et al. 1999). For example, on moonlit nights, Willets (*Catoptrophorus semipalmatus*) inhabit sand substrates and hunt fiddler crabs (*Uca* spp.) by sight, whereas on moonless nights they switch to muddy substrates and forage using tactile cues (McNeil and Rompré 1995).

Similar mechanisms may cause differences between diurnal and nocturnal flocking behavior and habitat use in golden-plovers and lapwings in agricultural landscapes. Understanding such differences is important, because wildlife managers often employ diurnal surveys as a means of identifying key sites and habitats, especially for waterbirds. However, differences between diurnal and nocturnal selection pressures mean that recommendations based on diurnal observations alone may be inadequate to manage a species. Therefore, we examined the degree to which nocturnal flocking behavior, abundance, activity, and habitat use differed from diurnal patterns.

METHODS

FIELD METHODS

The study area comprised 213 fields arranged around four road transects in southeastern Norfolk, United Kingdom (52.4°N, 1.1°E; 50 m above sea level). Up to 70% of the area was in cereal crops and <10% in grass, with seasonally variable quantities of bare tillage and stubble. During October to February 2000–2001 and October to March 2001–2002, paired diurnal and nocturnal surveys were performed close to the full- and new-moon dates (Astronomical Almanac 2000, 2001, 2002; see Acknowledgments). Paired surveys were used to identify differences in behavior between day and night while keeping other factors, such as weather, golden-plover and lapwing density, and habitat availability, constant.

Trial nocturnal observations in February 2000 showed that nocturnal surveys were more time-consuming than diurnal surveys, because each field must be scanned from multiple points. Also, some fields extended too far from the road to be thoroughly checked. Therefore, a random subset of 50 of the 213 fields was selected for nocturnal surveys. The selection was made after excluding a small number of fields that were too large or in which hedges blocked the view.

For the diurnal observations, all 213 fields were surveyed. Using a vehicle as a blind, we searched each field for golden-plovers and lapwings. Binoculars alone were sufficient to detect birds on most substrates except plough or sugar beet stubbles. A telescope largely overcame those detection problems, though small numbers of birds may still have been missed.

Nocturnal observations were performed using an image intensifier fitted with a 300-mm variable-aperture Nikon SLR camera lens and using a 1-million candle-power lamp fitted with an infrared filter for illumination. By this means, nocturnal birds and mammals were detectable to a range of 400 m. Thus, day and night methods were quite different: nocturnal surveys of the 50 fields required 5–10 h, compared with <6 h to cover all 213 fields during daylight. However, both methods were designed to maximize detection of birds under prevailing conditions and get the best information on distribution and abundance of lapwings and golden-plovers during day or night.

The following information was recorded for each field: habitat type, number of lapwings and golden-plovers in each flock, and activity (number feeding vs. loafing). Cloud cover, rainfall, and moon state (up–down; clear–obscured) were recorded on nocturnal surveys. A flock is defined as a distinct aggregation of birds in one part of a field, where the distance between flocks was greater than that between individuals within a flock. More than one flock could be found in one field. A field is defined as “occupied” if one or more individuals were present. Feeding birds were those actively foraging, as apparent from pause–travel foraging motion, scanning, or handling of prey. Loafing encompassed nonfeeding activities in which individuals were stationary (preening, sleeping, inactive but alert). The order in which transects were visited was randomized to avoid consistent biases. Diurnal surveys avoided the first and last hour of the day, and nocturnal surveys started at least one hour after dusk and were completed by 0200 hours. Nights with high wind, heavy rain, or fog were avoided, because such weather adversely affected the efficiency of the viewing equipment.

OTHER DATA SOURCES

Local ground-surface temperature (T_L) was recorded during most nocturnal surveys. Where not recorded, local temperatures were estimated using minimum (T_{MIN}) and maximum air temperature (T_{MAX}) (and the midpoint of these, T_{MID}) from the Institute for Arable Crop Research’s Broom’s Barn research station, 40 km southwest of the transects. Linear regression was used to determine the best relationship

between local ground temperature recorded at the time of surveys and those from the Broom's Barn archives (T_{MIN} , T_{MAX} , T_{MID}) so that missing values could be estimated.

ANALYTICAL METHODS

Percentage of field occupancy was calculated as the number of times a field was occupied divided by the number of times it was surveyed and available for occupancy (i.e. excluding completely unsuitable habitats such as maize [*Zea mays*], which is too tall for golden-plovers and lapwings; Gillings 2003).

Two analyses examined how diurnal and nocturnal abundance were related. The first compared the numbers of birds seen by day on all 213 fields and at night on only the 50 random fields. The second compared the total numbers of birds seen by day and by night on the 50 random fields, with the expectation of a 1:1 relationship. Because the 50 random fields accounted for 23% of all 213 fields (by area and number of fields), we expected a 1:0.23 relationship between day and night totals. Though the latter test makes the most direct comparison of totals, the former test was also performed because diurnal flocks are highly aggregated and a small sample of fields seriously underrepresents the actual population of birds using the study area by day. Totals for each survey were square-root transformed (Sokal and Rohlf 2000) and analyzed by linear regression. If any significant relationship existed between day and night totals, the slope was tested against the expectation of 1:1 or 1:0.23 as appropriate. After square-root transformation the 1:0.23 expectation for the second analysis translates to an expected slope of 0.48 (the square root of 0.23).

For flock size comparisons, all flocks recorded by day on the 213 fields were compared with the flocks recorded at night on the sample of 50 fields. (Too few flocks were found by day only on the sample of 50 fields to perform directly paired tests.) To test the effects of environmental conditions on golden-plover and lapwing activity, the proportion of golden-plovers or lapwings feeding was related to environmental variables using logistic regression performed in the SAS Genmod procedure (SAS Institute 2001). For this analysis, a sample was defined as the sum of all flocks located within a field, because these were all subject to the same

conditions, whereas flocks located in other fields (and hence at different times) were subject to differing conditions. For instance, ground temperature typically decreased after sunset, the timing of moonrise varied, and cloud cover rapidly changed both moon visibility and light levels. We selected the model with the lowest deviance as our best model. For overdispersed models in which deviance divided by degrees of freedom deviated widely from 1, the scale parameter was estimated by the square root of deviance divided by degrees of freedom. The effects of independent variables were tested using likelihood ratio tests, with significance tested against the chi-squared distribution. Variables were as follows: *Month* = October to March; *Moonphase* = full or new; *Mooncover* = no moon, cloud-covered, or up and clear; *Rain* = yes or no; T_{L} = ground temperature ($^{\circ}\text{C}$); and *Time* = hours since sunset.

Habitat use was determined by totaling the number of birds found on each habitat and converting to percentages. Habitat availability was accounted for by calculating Jacobs' selection indices (Jacobs 1974), which range from +1 for exclusive use to -1 for total avoidance. Data from the two winters were pooled because of the low number of encounters in some habitats. Nocturnal habitat selection was based only on the random subset of 50 fields. During the day, these fields contained few birds, so diurnal habitat use was based on records and habitats from the larger sample of all 213 fields.

RESULTS

SURVEYS AND TIMING

In 2000–2001 and 2001–2002, 22 paired diurnal and nocturnal surveys were made, including 11 during full-moon periods and 11 during new-moon periods. Moon illumination was close to, but not exactly, 0% or 100%: new-moon mean illumination = 5% (95% confidence interval [CI]: 2–8%), full-moon mean illumination = 95% (95% CI: 92–98%), and illumination differed significantly between full- and new-moon survey periods ($t = 21.9$, $df = 43$, $P < 0.0005$).

FIELD OCCUPANCY

Of the 50 fields surveyed at night, one was never available for occupancy, because it was

permanently overgrown with tall vegetation. Of the remaining 49 fields, 13 (27%) were never occupied at night, whereas many were occupied frequently ($\leq 81\%$ of nocturnal surveys). By contrast, during the day, 71% of fields were never occupied and maximum occupancy was only 27% of diurnal surveys. Frequency distributions of day and night occupancy differed significantly (Kolmogorov-Smirnov two-sample test, $KS_a = 2.7$, $P < 0.0001$). Day and night occupancy of individual fields were positively correlated ($r_s = 0.61$, $P < 0.0001$, $n = 49$), indicating that fields used by day were also used at night. However, occupancy was not equal and, on average, fields were occupied three times as often at night as by day (linear regression, $F = 297.0$, $df = 1$ and 47 , $P < 0.0001$, slope = 3.1 ± 0.2 ; Fig. 1).

GOLDEN-PLOVER AND LAPWING ABUNDANCE

Numbers of the two species fluctuated in synchrony (Fig. 2) during day ($r_s = 0.81$, $P < 0.0005$, $n = 22$) and night ($r_s = 0.52$, $P = 0.01$, $n = 22$). Seasonal trends in numbers were similar for day and night, although notably, in 2001–2002, golden-plovers were present on the transects at night despite being absent during the day (Fig. 2).

There was no significant relationship between day golden-plover totals for all 213 fields and night golden-plover totals for the 50 random fields ($F = 1.8$, $df = 1$ and 20 , $P = 0.19$). For lapwings, there was a significant positive

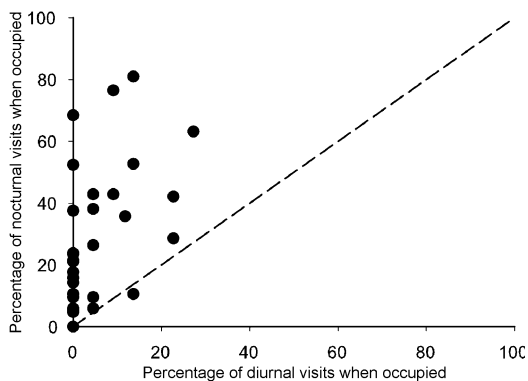


FIG. 1. Relationship between percentage of day occupancy and percentage of night occupancy by golden-plovers and lapwings on 49 fields. Dotted line indicates the expected 1:1 relationship if individual fields were used to an equal degree day and night.

relationship ($F = 66.1$, $df = 1$ and 21 , $r^2 = 0.76$, $P = 0.0001$; Fig. 3) and, on the square-root scale, the slope of 0.39 ± 0.05 was not significantly different from the expected slope of 0.48 ($F = 4.0$, $df = 1$ and 21 , $P = 0.056$). Thus, night totals were, on average, equal to 15% ($= 0.39^2$) of day totals, which was less than but not significantly different from the expected 23% based on the area sampled at night. Directly comparing day and night counts for only those birds seen on the random subset of 50 fields, there was no significant relationship between diurnal and nocturnal totals for either species (golden-plover: $F = 0.1$, $df = 1$ and 20 , $P > 0.75$; lapwing: $F = 0.3$, $df = 1$ and 20 , $P > 0.6$).

FLOCK SIZE AND COMPOSITION

Nocturnal flocks were significantly smaller (range: 1–450 individuals) than diurnal flocks (range: 1–4,000) (Table 1 and Fig. 4A). Nocturnal flocks were significantly larger at full moon than at new moon (Wilcoxon two-sample test: $z = 4.2$, $P < 0.0001$; Fig. 4B), whereas diurnal flocks did not differ in size between lunar phases (Wilcoxon two-sample test: $z = 0.4$, $P = 0.68$). Species composition of flocks differed between night and day. Only 17 of nocturnal flocks (5%) contained both species, compared with 91 of diurnal flocks (40%). Nocturnal mixed-species flocks were lapwing-dominated; in 9 of 17 flocks (53%), they accounted for $>60\%$ of individuals. Mixed diurnal flocks also were often dominated by one species, but with equal frequency: lapwings accounted for $\geq 60\%$ of individuals in 42% of flocks, and golden-plovers for 60% in 44% of flocks. There was no significant difference in single-species flock size between species, either at night (Wilcoxon two-sample test: $z = -0.6$, $P = 0.27$) or during the day (Wilcoxon two-sample test: $z = 0.12$, $P = 0.45$).

NOCTURNAL ACTIVITY

Golden-plovers were observed feeding on 20 of the 21 visits on which they were present, and lapwings on 19 of 20 visits (Fig. 2). The percentage of individuals feeding during each survey period did not differ between full- and new-moon phases (golden-plover: $\chi^2 = 0.28$, $df = 1$, $P = 0.6$; lapwing: $\chi^2 = 0.80$, $df = 1$, $P = 0.4$). Local ground temperature was recorded on 32 of the 45 dates on which visits were made. Comparing

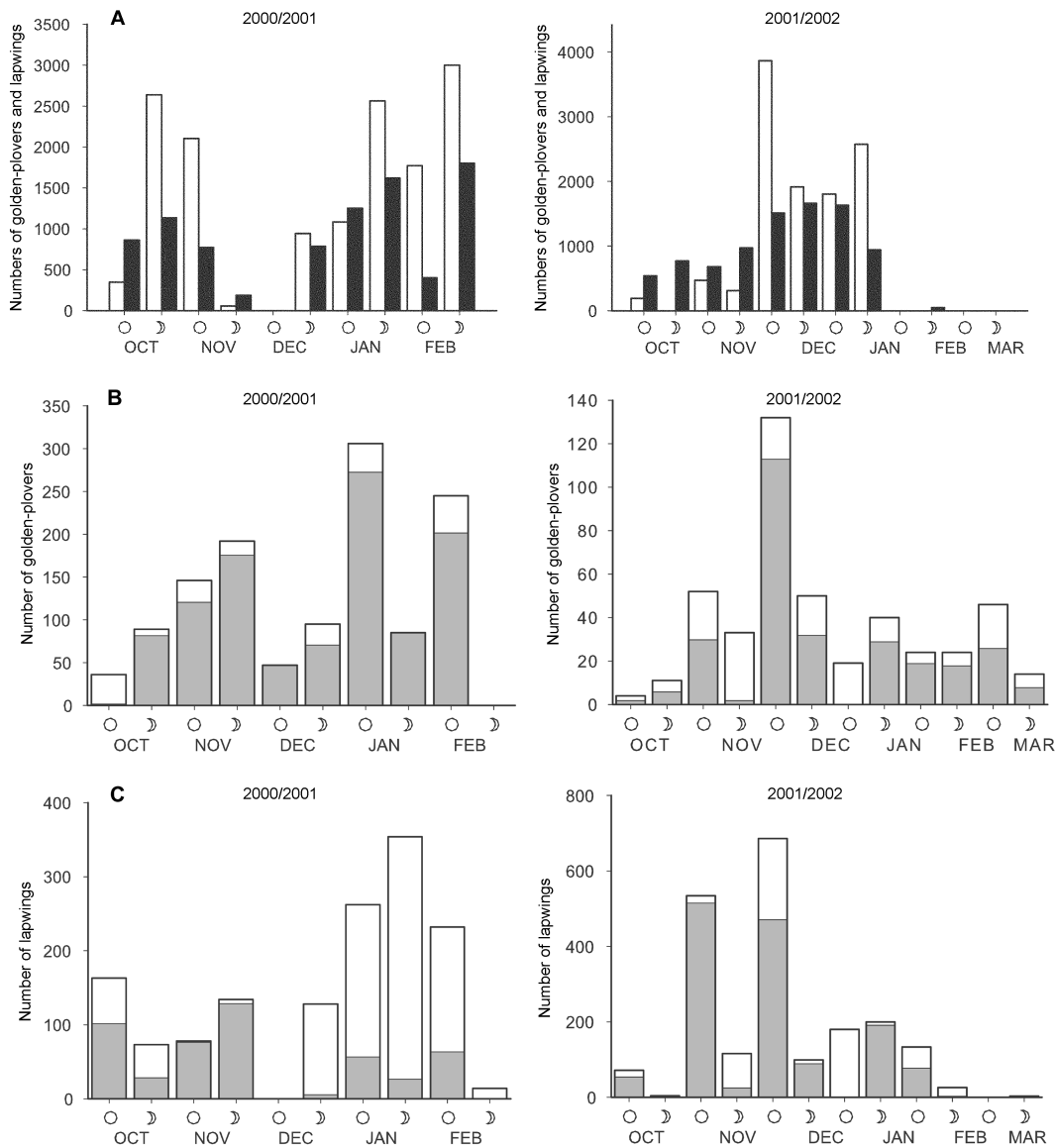


FIG. 2. Seasonal patterns of diurnal and nocturnal golden-plover and lapwing abundance and activity. (A) Diurnal abundance of golden-plovers (white bars) and lapwings (black bars) on all 213 fields. Nocturnal abundance and activity of (B) golden-plovers and (C) lapwings on the sample of 50 fields surveyed at night. In (B) and (C), bar height indicates total number recorded and the solid component indicates the number feeding. Circle and crescent symbols represent full-moon and new-moon survey periods, respectively, during each month.

measurements made on these 32 dates with data from Broom's Barn revealed that local ground temperature (T_L) was significantly related to T_{MIN} ($F = 181.9$, $df = 1$ and 30 , $r^2 = 0.86$, $P < 0.0001$), T_{MAX} ($F = 113.4$, $df = 1$ and 30 , $r^2 = 0.79$,

$P < 0.0001$) but most strongly to T_{MID} ($F = 186.2$, $df = 1$ and 30 , $r^2 = 0.86$, $P < 0.0001$). For analytical purposes, T_L values were estimated for all visit dates, using the relationship with T_{MID} ($T_L = -0.16 + 0.86 \times T_{MID}$).

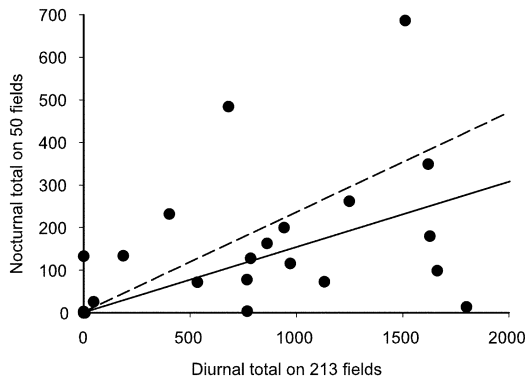


FIG. 3. Relationship between diurnal and nocturnal totals of lapwings on 213 and 50 fields, respectively ($n = 22$ paired visits). Given that nocturnal surveys covered only 23% of the study area, one would expect 23% of the day total at night (dotted line). The solid line is the actual relationship between diurnal total and nocturnal total.

Nonzero field counts where nocturnal activity was recorded totaled 118 records for golden-plovers and 103 for lapwings. These included full and new moons and both clear and cloudy conditions. The proportion of golden-plover individuals feeding did not vary significantly with season, moon phase, cloud cover, rain, or temperature (Table 2). Only the time since sunset (*Time*) was significantly (positively) related to the proportion of golden-plovers feeding (Table 2). By contrast, the proportion of lapwings feeding was significantly related to month, cloud cover of the moon, temperature (positive), and time since sunset (positive) (Table 2). With the exception of March, in which few flocks were located and activity was extremely variable, lapwing nocturnal feeding

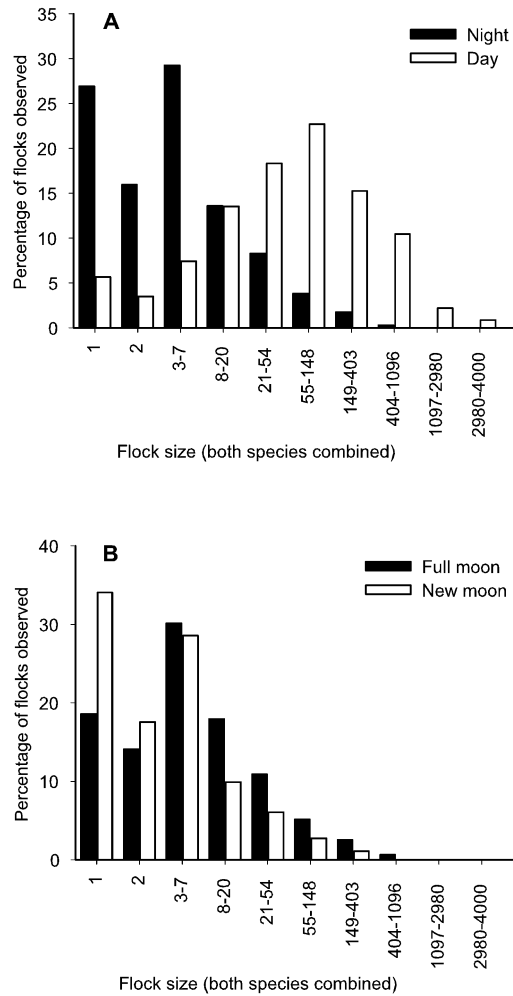


FIG. 4. Frequency distributions of flock sizes (A) during night and day and (B) at night on full- and new-moon nights. Samples sizes: (A) night = 338, day = 229 ; (B) full moon = 156, new moon = 182.

TABLE 1. Median flock sizes (with lower and upper quartiles in parentheses) and sample sizes (n) for categories of flocks recorded during nocturnal and diurnal surveys. Test statistic is the z normal approximation statistic for a Wilcoxon two-sample test (all $P < 0.001$).

| Flock category | Nocturnal | n | Diurnal | n | Test statistic |
|--------------------|------------|-----|--------------|-----|----------------|
| All flocks | 3 (1–9) | 338 | 59 (16–180) | 229 | $z = 14.0$ |
| Mixed-species | 37 (18–87) | 17 | 137 (73–381) | 91 | $z = -3.7$ |
| Golden-plover only | 3 (2–7) | 179 | 15 (8–202) | 14 | $z = 3.5$ |
| Lapwing only | 3 (1–10) | 142 | 27 (6–76) | 124 | $z = 7.8$ |
| Full moon | 5 (2–16) | 156 | 68 (20–179) | 114 | $z = 8.8$ |
| New moon | 2 (1–6) | 182 | 51 (13–176) | 115 | $z = 11.0$ |

activity was greatest in October and November (Fig. 5). This was not simply because of temperature: after controlling for temperature, month still made a significant contribution to explaining variation in feeding activity (Type 1 likelihood ratio statistic, $\chi^2 = 22.2$, $df = 5$, $P = 0.0005$). Though there was no significant effect of moon phase on feeding, the proportion of lapwings feeding increased with increasing moonlight resulting from changes in cloud cover (Fig. 5).

DIURNAL AND NOCTURNAL HABITAT USE

At night, 69% of golden-plovers were recorded on cereal (*Triticum* and *Hordeum* spp.) crops, 18% on oilseed rape (*Brassica napus*) crop, and 10% on sugar beet (*Beta vulgaris*) stubbles. During the day, 46% were recorded on cereal crops, 37% on bare-tilled ground, and 15% on sugar beet stubbles. Selection indices that controlled for habitat availability showed positive selection of bare-tilled ground and sugar beet stubbles by day, compared with positive selection of cereal and rape crops and sugar beet stubbles at night (Fig. 6A). Only 22% of lapwings fed on cereal crops at night, and the main habitats were sugar beet stubbles (23%) and bean (*Vicia faba*) stubbles (38%). By day, lapwings used habitats in a manner almost identical to that of golden-plovers. Habitat selection by lapwings differed subtly between day and night (Fig. 6B) and from that of golden-plovers.

DISCUSSION

The present study is the second to investigate the nocturnal behavior of lapwings (Milsom et al. [1990] is the other) and the first to investigate that of golden-plovers. Nocturnal foraging in both species occurred irrespective of moon phase, contrary to expectations based on diurnal activity. At night, golden-plovers and lapwings occurred in smaller flocks dispersed over a larger number of fields than during the day.

PLOVER ACTIVITY

The present study demonstrates nocturnal feeding by golden-plovers and lapwings during both full- and new-moon phases. This is contrary to predictions made from diurnal observations (Spencer 1953, Milsom 1984,

Barnard and Thompson 1985) and the previous nocturnal study (Milsom et al. 1990). Why nocturnal feeding should be prevalent across moon phases is unclear. It is possible that a large roosting flock existed on one of the unsurveyed fields, but this is unlikely for two reasons. First, the fields surveyed at night were not inherently unsuitable for roosting, because daytime roost flocks were located on these fields when cold weather prevented feeding. Second, casual nocturnal observations of a larger number of fields never yielded large roosting flocks and >90% of individuals were feeding. One possible reason for why golden-plovers and lapwings fed on new moons is that the study was conducted on cultivated fields. Farm practices affect surface-burrowing earthworm species more adversely than deep-burrowing species (Edwards and Bohlen 1996). The diurnal diet consists of small surface species, whereas the nocturnal diet consists of larger deep burrowers (Gillings 2003), and nocturnal feeding may be essential for meeting daily energy demands (supplementary hypothesis) or may be more profitable (preference hypothesis) (McNeil et al. 1992).

The prevalence of nocturnal feeding by lapwings was positively related to ground temperature, as predicted given that invertebrate prey, including earthworms, become inactive or retreat to deeper burrows in cold conditions (e.g. MacDonald 1983, Tomlin 1983). As in Milsom et al. (1990), increased cloud cover decreased lapwing feeding activity. This pattern was detected by crudely classifying the moon as visible, cloud-covered, or absent. It is likely that more precise patterns were obscured, because luminance may be greater when the moon is full and cloud-covered than when it is new and unclouded (Martin and de L. Brooke 1991). Despite the fact that they feed on the same prey items, golden-plovers showed no such patterns of activity with temperature, cloud cover, or month, perhaps because the two species use a different method of foraging. On some nights, small feeding flocks of golden-plovers were observed running across cereal fields, whereas lapwings always used the more methodical pause-scan method. Both species can locate prey by acoustic cues, but visual cues are more important (Lange 1968). Further work comparing visual and acoustic prey detection under differing light conditions would be valuable.

TABLE 2. Results of logistic regression relating the proportion of birds feeding at night to survey details and environmental variables. *Moonphase* = full or new; *Mooncover* = no visible moon, moon cloud covered, or moon clearly visible; T_L = local ground temperature; *Time* = time since sunset; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

| Variable | Golden-plovers | | | Lapwings | | |
|------------------|----------------|----------|----------|----------|----------|----------|
| | df | Deviance | χ^2 | df | Deviance | χ^2 |
| <i>Month</i> | 112 | 1,340 | 3.4 | 97 | 2,262 | 31.5*** |
| <i>Moonphase</i> | 116 | 1,376 | 0.4 | 101 | 2,916 | 2.8 |
| <i>Mooncover</i> | 115 | 1,356 | 2.2 | 100 | 2,656 | 12.8** |
| <i>Rain</i> | 116 | 1,380 | 0.1 | 101 | 2,936 | 2.0 |
| T_L | 116 | 1,378 | 0.3 | 101 | 2,320 | 29.3*** |
| <i>Time</i> | 116 | 1,304 | 6.8** | 101 | 2,867 | 4.5* |

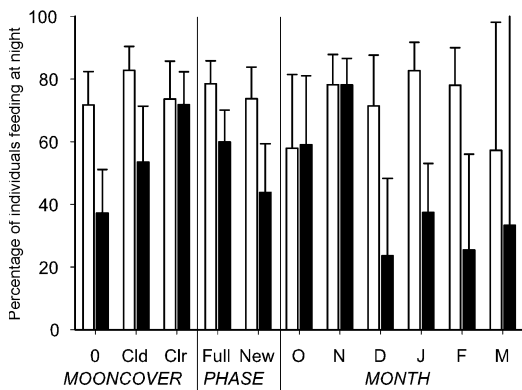


FIG. 5. Mean percentage of golden-plovers (white bars) or lapwings (black bars) nocturnally feeding (and Wald 95% confidence limits) summarized by *Mooncover* (0 = none, Cld = cloud covered, Clr = Clear), *Moonphase*, and *Month* (October to March). Values are back-transformed (logit) parameter estimates from generalized linear models.

In both species, feeding activity became more prevalent with time from sunset. This was contrary to expectation, given that ground temperatures and, hence, prey activity fall after sunset. A possible reason for the positive relationship is that no standard observations were made after 0200 hours. During one night when birds were feeding before midnight, extra observations made between 0300 and 0600 hours showed that most birds were roosting and that ground temperature had fallen to 0°C.

FLOCKING AND ABUNDANCE

Nocturnal flocks were considerably smaller than diurnal flocks. The size difference may

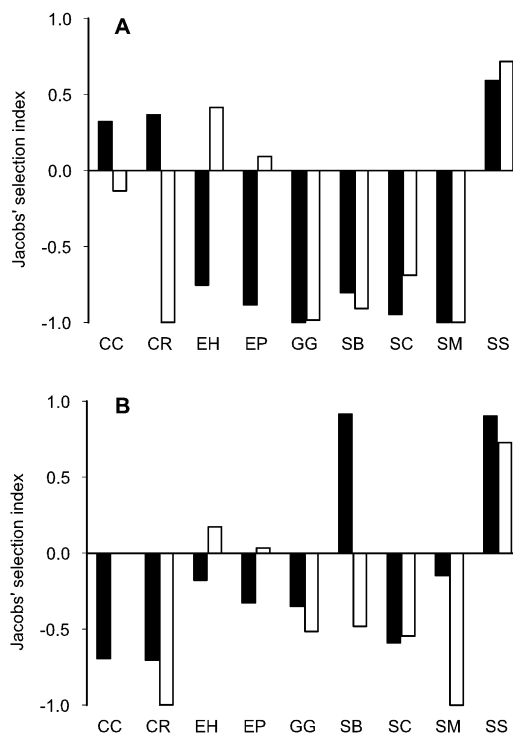


FIG. 6. Jacob's selection indices of habitat use by (A) golden-plovers and (B) lapwings during night (black bars) and day (white bars). Habitat codes: CC = cereal crop; CR = oilseed rape crop; EH = harrowed earth; EP = ploughed earth; G = grass; SB = bean stubble; SC = cereal stubble; SM = maize stubble; SS = sugar beet stubble.

be slightly exaggerated, because nocturnal surveys often required scans from multiple points on the perimeter of a field and may have "resolved" birds into several small flocks, whereas a diurnal scan from one point on a field

perimeter may not. Nonetheless, the magnitude of the difference between day and night flocks cannot be accounted for by this alone. Day-flocking is assumed to enhance predator detection; at night, predator detection by eyesight may be so limited that flocking is of little benefit. Also, nocturnal flocking may be costly if it attracts predators or if high densities of golden-plovers reduce intake rates through passive interference. Nocturnal flocks during full-moon periods were larger than those found during new moons, perhaps because the full moon gave flocking an antipredatory benefit or because birds searching for good foraging conditions could find successfully feeding birds more easily under a full moon. Most nocturnal flocks contained only one species, whereas day flocks were typically mixed. By day, golden-plovers parasitize lapwings by using them as cues to rich feeding areas (Barnard and Thompson 1985), but this is presumably more difficult in darkness (nocturnal feeding flocks were typically silent).

At night, golden-plover and lapwing flocks were distributed over more fields than during the day and night populations were not always predictable from day populations. For instance, golden-plovers were present on the study area at night during January–March 2002, yet the nearest day flock was ~6 km away. Diurnal observations on consecutive days and observed daytime movements confirm that movements of ≤ 15 km occurred regularly. This makes assessing the area requirements of these two species from diurnal surveys alone unreliable. Arguably, given that more than half the daily energy requirements may be met from nocturnal feeding (Gillings 2003), where these birds feed at night may be at least as important as their diurnal distribution.

HABITAT USE

Like studies of other nocturnally active shorebirds, the present study shows subtle differences in habitat selection between day and night. Furthermore, whereas the species use broadly the same habitats during the day, they differed from one another at night. Notably, grass fields, usually thought to be preferred habitats for feeding (e.g. Barnard and Thompson 1985), were avoided both day and night. The causes of habitat shifts between day

and night feeding and the difference between species probably involve differences in predator detection and nocturnal prey abundance, availability, and detectability. No predation events were seen, so it is difficult to determine to which predators golden-plovers and lapwings may be responding; furthermore, the effects of predators may be indirect. For instance, one potential predator is the red fox (*Vulpes vulpes*), which may feed on birds, rabbits (*Oryctolagus cuniculus*), or earthworms (MacDonald 1987). The climatic correlates of activity of red foxes foraging on earthworms (MacDonald 1983) are the same as those presented here for golden-plovers and lapwings. Therefore, the nights and sites that are most suitable for golden-plover and lapwing foraging may also be those that are most attractive to foxes. On several occasions, rabbits, foxes, golden-plovers, and lapwings were seen simultaneously in the same field. Understanding the mechanisms of predator detection and avoidance at night will be important in explaining nocturnal patch use.

In conclusion, the present study clearly demonstrates differing patterns of flocking behavior, species associations, habitat, and field use between day and night by golden-plovers and lapwings. Such differences have a firm theoretical basis, yet few studies have considered the consequences of differing diurnal and nocturnal behaviors. Throughout Europe, diurnal surveys of the distribution of shorebirds are used to delimit habitats and sites for protection (e.g. Stroud et al. 2001). However, if the results of this study are widely applicable, these protected sites may be of insufficient size and limited in habitat composition. Undertaking thorough nocturnal studies of all shorebird species is impractical, but understanding the processes leading to switches in behavior and patch use may make it possible to identify the species most liable to adjust their behavior and the habitats most likely to change in relative importance.

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