Habitat change and timing of dusk flight in the Eurasian woodcock: a trade-off between feeding and predator avoidance?

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Eurasian woodcock (*Scolopax rusticola*) over-wintering in northern Spain follows a pattern of daily movement from diurnal sites in woodlands to nighttime sites in grazed fields, congruent with previous reports on other European populations. Fields have a much higher abundance and biomass of earthworms, the main prey of woodcock, than woodlands, but are only used by birds at night, when they emerge about 30 minutes after sunset. Emergence time was quite uniform among fortnightly periods except for the second half of November when it was earlier, probably reflecting extended activity resulting from the higher energy requirements of migrating birds. Woodcock emergence time relative to sunset was negatively related to illumination, so that birds moved earlier when the sky was overcast. Also, birds tended to move earlier at low air temperatures, a pattern which is to be predicted since woodcock have higher energy requirements at low temperatures because of the increased cost of thermoregulation. Emerging late, at low light intensity, avoids exposure to raptors but results in reduced energy gains and therefore the timing of moving to feeding fields may be modified by energy considerations. We discuss the idea that there is a divergent spatio-temporal gradient of food and safety between woodlands and fields and, therefore, that predation risk is an important determinant of the timing of evening emergence of over-wintering woodcock. Thus, their daily activity cycle would reflect a trade-off between feeding and predator avoidance. Special features of the visual fields of the woodcock, allowing detection of predators at long distances, and chemoreceptors in the bill enabling detection and capture of prey by probing using non visual cues, comprise adaptations that facilitate successful feeding at night with reduced predation risk.

Introduction

Feeding and predator avoidance are frequently conflicting (Glück 1987, Lima & Dill 1990, Sih 1993, Eklöv & Halvarsson 2000). In order to gain energy and to reduce the risk of death, foraging decisions of prey are modulated according to habitat patchiness in levels of predation risk and food abundance or quality, and this modulation frequently involves the choice of

particular combinations of time and habitat to forage (MacArthur & Pianka 1966, Gilliam & Fraser 1987). Night feeding in profitable habitat patches, which are different to the diurnal roost sites, is widespread among shorebirds and is probably the most common behaviour used in the trade-off between energy gain and predator avoidance (Mouritsen 1992, Keitt *et al*. 2004, Lourenço *et al*. 2008).

The Eurasian woodcock (*Scolopax rusticola*) is a long-billed terrestrial wading bird (Charadriiformes), which primarily forage by probing in soft substrates for earthworms and other invertebrates (Hoodless & Hirons 2007). The efficiency of this feeding behaviour depends upon prey availability and soil penetrability, making these the key elements in the selection of feeding sites (Green *et al*. 1990, Hoodless & Hirons 2007). In winter, the Eurasian woodcock shifts its daily activity between two habitat types that differ in food quality and predator pressure. From late autumn to early spring woodcock remain in woodlands by day and fly at dusk to feed in nearby fields, this change being thought to occur because food is more abundant in fields where, by day, they are much more vulnerable to avian predators (Hoodless 1995, Duriez *et al*. 2005a, 2005b). Apart from the costs and benefits associated with each kind of habitat, movement between habitat patches in itself represents a critical event since, for cryptic animals, moving increases the probability of detection by predators and, thus, predation risk (Morey 1990, Kortet & Hedrick 2004). Movements by animals in open spaces, such as woodcock flying from woody habitats to open fields, make them detectable and can increase predation risk (*see* Green *et al*. 1990, for *Gallinago gallinago*). Consequently, predation has been recognised as an important factor influencing emergence time and activity patterns in many nocturnal animals. Furthermore, predation by raptors that rely on vision for hunting has been proposed as a major selective force in the evolution of nocturnality in many birds (e.g., McNeil *et al*. 1992, Keitt *et al*. 2004) and mammals (e.g., Speakman 1995, van Schalk & Griffiths 1996, Duverge *et al*. 2000).

Our general hypothesis is that woodcock face a trade-off between feeding and predation avoidance, of which nocturnal foraging is an indication. Our study had two objectives: (1) to compare food availability in two contrasting, yet neighbouring, biotopes used daily by woodcock during winter, and (2) to investigate the timing of dusk flights made by birds moving from woodlands to grazed fields in relation to the time of sunset and to luminosity, in order to evaluate the possible functional significance of night foraging and daily habitat shifts.

Material and methods

We investigated Eurasian woodcock over-wintering in the lowlands (200 to 300 m a.s.l.) of central Asturias (northern Spain). The study was conducted in a mosaic of small forests (mean size ± SD: 14.14 ± 12.56 ha, range 1.79–55.10 ha) and cattle grazed fields located in an area of ca. 250 km^2 around Noreña (43°23´N, 5°42´W). Despite the existence of a small reproductive population in high elevation areas of the neighbouring Cantabrian mountain range, our sample was probably composed almost exclusively of migratory individuals coming from northern countries. Woodcock were caught in mistnets and by spotlighting feeding fields at dusk and were fitted with radio transmitters (9–11 g, Biotrack Ltd.). Radio-tagged birds were located two or three times per week both during the day and around sunset (typically between one hour before and one hour after sunset), by using a receiver in conjunction with a hand-held three-element Yagi antenna. Only birds that yielded information of more than five day-night locations were considered to describe patterns of habitat shift and distances covered.

From mid-November to mid-March, covering most of the over-wintering time of migratory woodcock in northern Spain, one experienced observer (L.P. most frequently) surveyed the forest edge and the neighbouring grazing fields to detect woodcock flying from the woodlands. Surveys were performed at least three times per week during the winters of 2007–2008 and 2008–2009, changing the observatory every day in order to avoid pseudo-replicating the observations. Radio-tagged birds were excluded from this part of the study. Watching positions were established at least one hour before the expected

time of the first flight (according to information provided by the radio-tagged birds) and continued until half an hour after detecting the last movements. The time of first woodcock entry was recorded to the nearest minute and related to the time of sunset for analyses. Cloudiness was assessed by dividing the sky into eight fields, although these were amalgamated into two broad categories for analysis: cloudless (classes 0–4; less than half of the sky covered) and clouded (classes 5–8; more than 50% of the sky covered). In addition to recording general cloudiness, for one part of the surveys conducted during the winter 2008–2009, open-sky light levels were recorded to the nearest 0.1 lux with a digital light meter. Light levels were recorded 15 min after sunset, approximately the time at which woodcock initiate dusk activity, and when each bird appeared. Data on local temperature at sunset (to the nearest 0.01 °C) were obtained from the State Agency of Meteorology (Oviedo station).

During dusk surveys and when spotlighting at night to catch birds, we detected several predatory birds and mammals reported to include woodcock into their diet (*see* Discussion for detailed references): *Falco peregrinus*, *Buteo buteo*, *Accipiter gentilis*, *A. nisus*, *Strix aluco*, *Vulpes vulpes*, *Martes martes* and feral cats. Tawny owls (*Strix aluco*), foxes (*Vulpes vulpes*) and feral cats were most commonly seen in the fields at night. Tawny owls and barn owls were captured in mist nets along with woodcock, and tawny owls were seen chasing woodcock although no successful attacks were observed. Other potential predators observed were *Falco tinnunculus*, *Tyto alba* and *G. genetta*.

We determined earthworm abundance in sites used by woodcock both during the day and during the night. Earthworms were sampled only during the day. In addition to locations provided by radio-tagged woodcocks (only one for each individual to avoid pseudoreplication of the data), diurnal sites used by woodcock within woodlands were determined by flushing birds out with trained pointing dogs, while nocturnal feeding sites were located by spotlighting the neighbouring fields. We selected 25 diurnal (woodlands) and 25 nocturnal (grazed fields) woodcock sites for earthworm sampling. Earthworm abundance was sampled from two 60 ×

60 cm plots per site, and from two other plots at sites randomly chosen within the same kind of structural habitat situated 300 m away from each woodcock site (25 sites in woodlands and 25 in grazed fields). Samples were taken by using a combination of manual and chemical extraction after clearing surface vegetation (Edwards & Lofty 1977); three successive baths of increasing concentrations of formalin (from 0.2% to 0.4%) were applied at 15-min intervals and the emerging earthworms were counted and collected. Earthworm sampling was completed by hand sorting the soil to a depth of 10 cm. Earthworms were preserved in 70% ethanol and later weighed to the nearest 0.001 g.

Data were checked for normality (Kolgomorov-Smirnov test) and for homocedasticity (Bartlett's test) prior to further statistical analysis, and we performed logarithmic transformations where necessary to satisfy the assumptions of parametric tests. We used a two-factor analysis of variance to test for the effects of period (eight sampling periods from November to March) and cloudiness on the timing of dusk emergence. As data corresponding to the fortnightly periods in the two years of study were similar, years were combined for analysis. Data on earthworm abundance and biomass in woodland and field samples were highly skewed and did not improve with simple transformations; for this reason, these data were analysed using the nonparametric median test followed by the Mann-Whitney test for between-pair comparisons. All tests were two-tailed.

Results

We radio-tagged 22 woodcock individuals of which 14 gave more than five recordings of dusk movements and were included in this study, 6 birds were lost to predation, and the signal for 2 other birds was lost few days after tagging without giving enough data to be analysed. The movement pattern of most of the radio-tagged birds was very similar: by day they were located in habitats with high tree or bush cover and moved by flying a short distance to grazed fields at sunset. Only one bird frequently remained in a moist peat bog within the wood at night (9 times
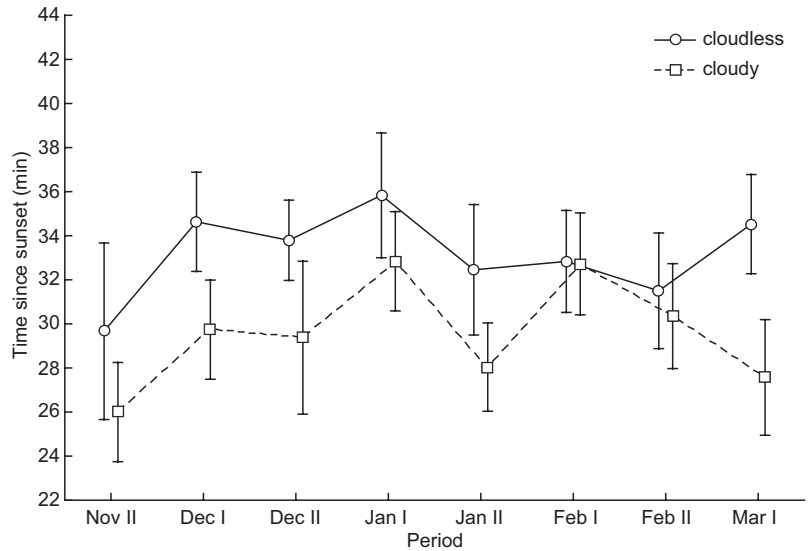
Fig. 1. Variation in emergence times (minutes after sunset) of woodcock grouped by fortnightly periods from the second half of November (Nov II) to the first half of March (Mar I) and according to cloudiness. Means and 95% confidence intervals are shown.

out of 21 nocturnal locations) and another two occasionally moved a few tens of meters from roosts near the woodland edge to nearby fields by walking instead of flying. Mean distances covered from diurnal roost to fields ranged from 147 to 865 m (average of mean distances ± SE: 347.05 ± 55.46 m, $n = 14$) and, excluding the data from one bird that frequently remained within the woods at night, woodcock roost in the woodland at an average distance of 64.32 ± 42.72 m from the edge.

Time of evening emergence was clearly defined: more than 90% of woodcock moved from 25 to 40 min after sunset on clear days (mean ± SE: 33.65 ± 0.40, $n = 135$) and from 15 to 35 min after sunset on cloudy days (29.55 ± 0.47, $n = 142$). Considering eight fortnightly periods throughout the main over-wintering stay of woodcock in northern Spain, there was a clear effect of sky cover (ANOVA: $F_{1,261} = 41.049$, $p < 0.001$) and period ($F_{7,261} = 4.261$, $p < 0.001$) on the time of emergence after sunset, without a significant interaction between these factors ($F_{7,261} = 1.588$, $p = 0.239$) (Fig. 1). However, the significant effect of period on the timing of emergence after sunset was mainly attributable to low values (i.e., earlier emergence) during the second half of November on cloudy days, as this is the only period exhibiting significant differences (a posteriori Scheffé test; $p < 0.05$).

Woodcocks emerged at an average luminosity of 1.93 lux (SE = 0.32), and the light level at emergence did not differ between cloudy and cloudless days (ANOVA: $F_{1,36} = 0.165$, $p = 0.687$). There was an obvious negative correlation between direct values of evening emergence time and illumination at that time ($r = -0.698$, $p < 0.001$, $n = 277$), as late movements occur at lower ambient light. However, a significant positive relationship was found between the delay of first sighting of woodcock after sunset and values of luminosity at sunset ($r = 0.516$, $p < 0.01$, $n = 38$), further indicating that birds tended to move later on brighter days. Air temperature at emergence ranged from 2.60 to 17.60 °C (mean ± SD = 8.94 ± 2.84 °C; Fig. 2). There was a significant positive correlation between emergence time and air temperature on cloudy nights ($r = 0.226$, $p = 0.007$, $n = 140$; Fig. 3) but not on cloudless nights ($r = 0.117$, $p > 0.1$, $n = 137$). Again the data from November contributed heavily to the correlation for cloudy nights ($r = 0.455$, $p = 0.022$, $n = 25$).

The median test revealed highly significant differences in earthworm abundance ($\chi^2 = 11.175$, df = 3, $p = 0.011$) and especially in biomass ($\chi^2 = 31.155$, df = 3, $p < 0.001$) among the samples taken in woodlands and grazed fields. Overall, the number and biomass of earthworms caught was considerably higher in fields than in
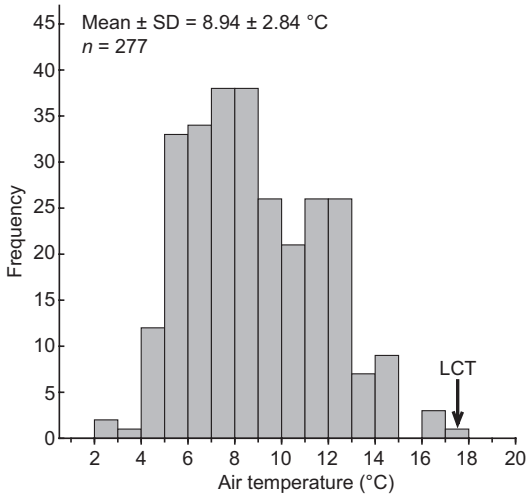
Fig. 2. Frequency distribution of air temperature at the sunset emergence of woodcocks. The arrow indicates the position of the Lower Critical Temperature (LCT) according to Duriez *et al.* 2004a.

woodlands (Mann-Whitney *U*-test: $p < 0.001$ in both cases; Fig. 4). Within each of these habitat types, localities occupied by woodcocks tended to have higher abundances and biomasses of earthworms than randomly chosen locations; the differences being statistically significant for grazed fields ($Z = 2.028$, $p = 0.042$ for earthworm abundance; $Z = 2.726$, $p = 0.006$, for earthworm biomass), but not for woodlands (respectively: $Z = 1.380$, $p = 0.168$; $Z = 1.387$, $p = 0.165$).

Discussion

Our results indicate that woodcock mainly use woodlands during the day and grazed fields during the night, congruent with previous reports for other European populations (Hirons & Bickford-Smith 1982, Duriez *et al.* 2005a, Hoodless & Hirons 2007). Woodcock feed mainly on earthworms and, in winter, grazed fields have a much higher biomass of earthworms than woodlands as well as smooth ground suitable for probing. In addition, earthworms exhibit vertical migration and are closer to the soil surface at night, so the amount of food available to woodcock should be higher at night (Butt *et al.* 2003). We therefore suggest that the woodcock's daily activity pattern occurs because food is more abundant and available in fields than in woodlands, which is reinforced by the fact that, in this study, grazed fields selected by woodcock at night had higher earthworm abundances than randomly selected sites. Interestingly, Duriez *et al.* (2005a) demonstrated that woodcocks that stayed permanently in the woods fed mainly during the day, whereas individuals that alternate between the woodlands (during the day) and the fields (during the night) fed mainly during the night. Moreover, woodcock hardly use meadows as feeding habitat in summer (Hoodless & Hirons 2007; author's unpubl. data), probably due to the fact that soil desiccation greatly reduces earthworm availability (Peach *et*
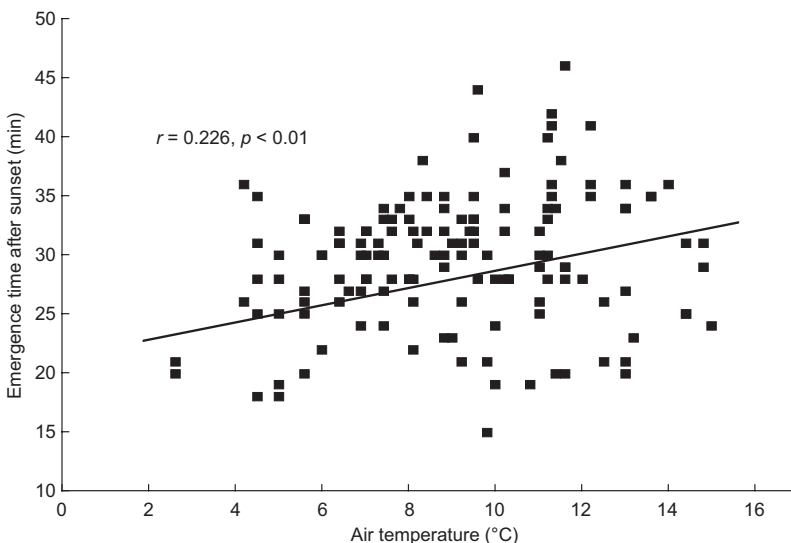

Fig. 3. Relationship between emergence time relative to sunset and air temperature on cloudy nights ($n = 140$).

al. 2004). This complex scheme of habitat use may be primarily related to patchiness in food abundance, but, given the energy disadvantages of restricting foraging activity to the night, some additional reasons are needed to explain why fields are never used during the day. The fact that earthworms were more active and closer to the surface at night is probably not the main explanation for nocturnal feeding in fields: woodcock can feed on earthworms by day within woodlands, which are rich in food (Duriez *et al.* 2005a) and do not forage in meadows by day even when rain induces high earthworm surface activity (Chuang & Chen 2008). Predation risk is known to cause shifts in foraging time and behaviour, even at the cost of reducing the forager's food consumption (Sih 1993, for shorebirds *see* McNeil *et al.* 1992, Piersma *et al.* 2006, Pomeroy 2006), and below we shall discuss some environmental relationships of the timing of moving from diurnal roosts to fields, which suggest that predation risk avoidance could be an important factor in understanding this apparent paradox.

Our results clearly indicate that, throughout the over-wintering period (from November to March), all but one bird flew to the grazed fields every day at dusk, and flew earlier when the sky was overcast, so that flight times relative to sunset were negatively related to illumination. Emergence time was quite uniform between fortnightly periods except for the lower values corresponding to the second half of November, perhaps reflecting extended activity because of the higher energy requirements of recently arrived birds or transients at a migration stopover. Presumably, since the efficiency of diurnal raptors declines abruptly with darkness (Fox *et al.* 1976), woodcock use illumination levels as an indirect environmental cue to assess predation risk (*see* Vásquez 1994). For prey animals to successfully negotiate the trade-off between predation and starvation, a realistic assessment of predation risk is vital. Direct assessment is risky, as it involves actual predator confrontation, and thus strong selection for the detection of indirect cues is to be expected. Indirect cues of predation risk, such as illumination or habitat structure, convey information about risk from multiple potential predators and can provide an integrative assessment of predation risk (Orrock *et al.* 2004).
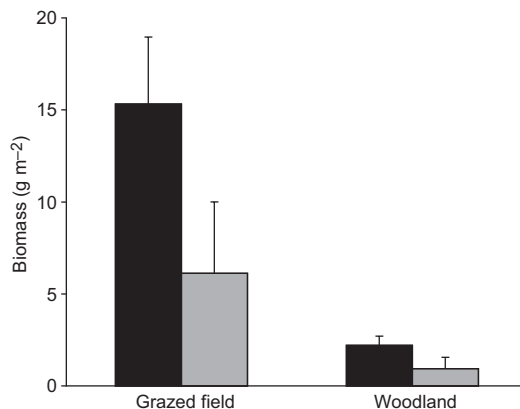

Fig. 4. Mean (+ SE) earthworm biomass (g m^{-2}) in grazed fields and woodlands. Black bars represent sites where woodcocks were observed while grey bars are randomly selected sites.

Movement breaks the imperceptibility of cryptic animals and is, in addition, a pervasive prey-attack eliciting stimulus for most visual predators (Curio 1976). Green *et al.* (1990) stressed that movement from the nest to feeding sites of female *Gallinago gallinago*, a close relative of woodcock, are likely to draw the attention of predators. Furthermore, many studies have reported higher rates of predation close to habitat boundaries (e.g., McCollin 1998, Morris & Gilroy 2008). Therefore, moving from the day refuge to the night feeding fields across the forest edge would be particularly risky and woodcock would be expected to minimize the time and conspicuousness of these movements by choosing roosting spots close to feeding areas and also by moving at low light levels.

Temperature was found to be a second environmental factor influencing emergence time: birds moved earlier from roost woodlands to feeding fields on cold days. Duriez *et al.* (2005a) also found clear indications that the intensity of nocturnal feeding activity increases when air temperature decreases, and some studies reported congruent results in other shorebirds (Systad & Butsnes 2001). This pattern is to be expected since woodcock have higher energy requirements at low temperatures due to the increased cost of thermoregulation (Boos *et al.* 2005). The relationship between air temperature and emergence time was particularly strong in the second fortnight of November, reinforcing

the above interpretation, as migrant birds would also have high energy requirements. Such earlier emergence at low temperatures or at life stages of high energetic demands, during pregnancy or lactation for example, has been repeatedly observed in many bat species (*see* Duvergé *et al.* 2000, and references therein). In addition, anticipatory night feeding activity on cold days may be important to allow the gathering of food before the soil becomes frozen, since woodcock have difficulty probing for prey in frozen ground (Gossman & Ferrand 2000). It is worth noting that all but one out of 277 air temperatures recorded at sunset emergence were lower than the Lower Critical Temperature (LCT; 17.5 °C, Duriez *et al.* 2004a; *see* Fig. 2), below which homeotherm animals can not maintain their core temperature constant without increment of metabolic heat production. Typically, temperature will decrease even more throughout the night and will increase from dawn onwards. Therefore, considering that birds foraging on the ground exposed to wind have higher energy expenditure than resting birds (Zerba *et al.* 1999), and that low temperatures increase the effects of wind on metabolic costs of thermoregulation (Wolf & Walsberg 2000, Bakken *et al.* 2002), we conclude that nocturnal activity cannot be understood by only considering the physical environment.

Woodcock are vulnerable to predation by a number of avian and mammalian predators. Avian predators would be the main risk for birds flying or foraging in open spaces; for example, among the species found in our woodcock surveys, *Falco peregrinus* is an important predator of woodcock in winter (Drewitt & Dixon 2008), and *Accipiter gentilis* (Widén 1987), *Accipiter nisus* (Hoodless & Hirons 2007), *Buteo buteo* (Reif *et al.* 2001), and *Strix aluco* (Hoodless 1995) are known to include woodcock into their diet, although they generally only represent a small proportion of the prey. The fox have been reported as a woodcock predator in our study area (Braña & del Campo 1980) and Duriez *et al.* (2004b) attributed most cases of predation in fields during the night to terrestrial predators such as foxes, feral cats or mustelids. We also found high predation rates and similar predator

identity in our study population, with 6 out of 22 tagged woodcocks consumed by carnivorous mammals (5) and birds (1). However, both these studies were based on the recovery of radio-tagged animals which were perhaps handicapped by the tag attachment devices in some cases (almost certainly in two of our cases), and in our records we are unable to separate true predation from carrion consumption or the capture of weakened animals.

Visibility has been proposed as an important habitat feature in relation to anti-predatory defence (Rodríguez *et al.* 2001, Tillmann 2009). Grazed fields are generally considered high risk habitats for the prey of diurnal avian predators because of wide visual areas and the absence of refuges (Ylönen *et al.* 2002, Orrok *et al.* 2004). At night, woodcock are mainly at risk from predators such as owls or terrestrial mammals, which are only able to catch by stealth (Rogers *et al.* 2006; *see* also Tillmann 2009, for *Perdix perdix*). The tactile feeding mode of woodcock, using the bill to probe into the ground, would make them highly vulnerable when confronted with these predators. However, the particular position of the woodcock's eyes, placed laterally and high in the skull, provides panoramic vision in a horizontal plane and throughout the hemisphere above the head (Martin 1994, Schwab 2001), thereby facilitating predator detection. One potential cost of nocturnal feeding is the difficulty of detecting and capturing prey, but this cost is largely diminished in woodcock by the use of non visual senses for prey detection (McNeil & Rodríguez 1996). The bill of the Eurasian woodcock is placed in the periphery of the frontal binocular field, as typically occurs in species whose foraging is mediated by non-visual cues. In fact, the bill tip is outside the visual field, excluding visually guided precision-pecking (Martin 1994, Martin & Piersma 2009). In addition, hearing is thought to contribute to prey detection (Fraguglione 1983). Thus, we conclude that, in woodcock, the features of the visual fields, together with the capacity to detect and capture prey by probing into the substrate using tactile cues, comprise an adaptive syndrome that facilitates successful feeding at night with reduced predation risk.

Acknowledgements

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