Communication of Eurasian Woodcocks in dark environments

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Abstract Species with cryptic plumages and behaviour face a dilemma: how do they attract attention when they want to? The ‘roding’ behaviour of male Eurasian Woodcocks *Scolopax rusticola* is well documented, as is the highly reflective white undersides of the tail tips. However, the behaviour of females in response to roding males, and the way the two sexes communicate,

remains poorly understood. In this paper, we show that females on the ground attract the attention of roding males by making a soft call and flicking the white tail-feather tips upwards.

Introduction

Many prey species have evolved traits to avoid detection from predators. They tend to be inconspicuous – that is, they are generally non-vocal, have cryptic plumage and reduced movement to remain hidden. This is especially true for ground-nesting species, such as female gamebirds and ducks, which are at risk from both aerial and ground predators (Troscianko *et al.* 2016; Stevens *et al.* 2017). However, concealment also renders these birds well hidden from conspecifics, potentially limiting mate choice and intraspecific communication. Hence, cryptic species require channels of communication that are used only in specific contexts.

This conflict between concealment and conspicuousness is most apparent in crepuscular and nocturnal prey species. Good camouflage is essential, particularly during the day. However, to be conspicuous in the dark, with an otherwise cryptic plumage, presents a problem. Many nocturnal species, such as owls and nightjars, communicate vocally with conspecifics. Some display white plumage patches, which are still visible in poor light and at a distance, such as the white wing-flashes on the wings and tail of nightjars and stone-curlews (Bettega *et al.* 2013; Penteriani & Delgado 2017). The white patches, which are generally hidden or less visible on the bird's closed wing, are often displayed only during flight, when these birds may be less vulnerable to predation than on the ground. However, because nocturnal species are difficult to observe, the behavioural ecology of these groups is generally poorly understood.

In this paper, we describe how the Eurasian Woodcock *Scolopax rusticola* has solved the conflict between concealment and conspicuousness. During the breeding season, Woodcocks inhabit woodland, which is darker in dim light than non-wooded habitats and offers a particular ambient light, making the use of visual channels of communication difficult (Endler 1993). Nevertheless, Woodcocks do use visual communication, in combination with vocalisations.

We previously described the morphological traits that allow Woodcocks to signal to conspecifics at night, by using very bright white plumage patches (Dunning *et al.* 2023). Yet, the behavioural ecology of how these patches are used to communicate, as well as other means of communication (beyond the well-described 'roding' display flights of the male), is poorly understood.

We used extensive field observations and sound recordings from a population of Woodcocks in the Jura Mountains, Switzerland, to describe the behavioural ecology of Woodcock communication at dusk, and the specific channels they used to communicate.

In this paper, we first describe visual and acoustic means of communication during courtship, including from the poorly described female perspective; secondly, we summarise how Woodcocks combine these visual and vocal signals to communicate in low-light environments.

Means of communication

Visual communication

The only non-camouflaged areas in a Woodcock's plumage are the white

spots at the tips of the tail feathers. The modified feather structure in this area of the tail feather was first described by Russian ornithologists (Borodulina & Formosow 1967): the rami (barbs) are broadened, flattened and overlapping, preventing light from passing through the feather vane, while the arrangement of the rami also increases the surface area for light reflection (Dunning *et al.* 2023). The white spots are visible only on the underside of the feather because on the upper surface the rami are covered by greyish-brown barbules (fig. 1). On the brown part of the tail feathers, the rami consist of thin barbs that are evenly spaced by the barbules (fig. 1), as elsewhere in the Woodcock's plumage and as is typical for other birds.

Fig. 1. Eurasian Woodcock *Scolopax rusticola* tail feather shown from above and from below.

The flattened rami of the white tip are arranged like Venetian blinds and

positioned at the optimum angle for light reflectance (Dunning *et al.* 2023). The sides of the white feather tip either side of the rachis (shaft) are both slightly concave and their barbs are inclined at opposite angles, such that light is reflected in different directions (fig. 2; plates 11 & 12). When the tail is moved (e.g. flicked) or a bird passes overhead, this concave structure likely reflect light maximally, at least from some parts of the tail, or it may have a sparkling or blinking effect, all similar to a cat's-eye reflector.

fig. 2

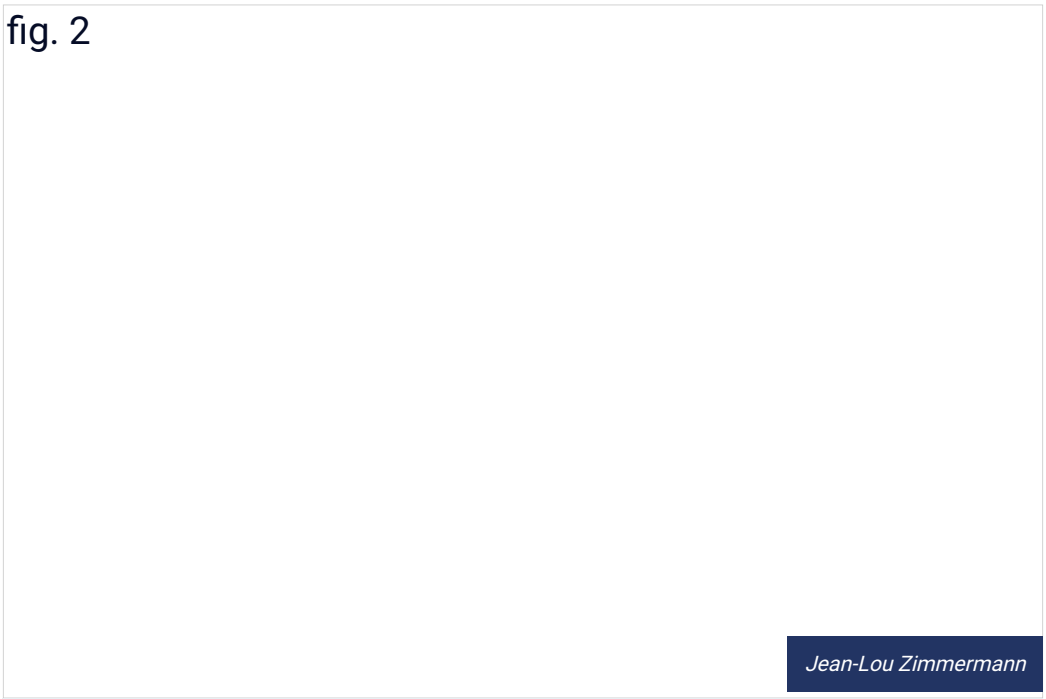

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Fig. 2. Each side of the white spot (left and right of the rachis) on the tip of a Eurasian Woodcock's tail reflects light in different directions. In dim light, only the side reflecting light directly towards the observer appears brilliant white. Here we show this directionality by illuminating a feather so that light is reflected maximally to the observer from one or the other side.

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11 & 12. The two sides of the white spot on the tip of the tail of Eurasian Woodcocks *Scolopax rusticola* reflect light in different directions. Hence, in dim light, only the side reflecting light towards the observer appears brilliant white, as shown on most of the tail feathers of the flying bird and on the three outermost rectrices on the part of the tail highlighted on the sitting bird (see also fig. 2).

The white rami contain a complex network of photonic cells – networks of keratinous nanofibers and scattered air pockets, entirely lacking melanosomes, which produce and store melanin in other feathers (fig. 3).

This particular composition of keratin and air enables very efficient light reflectance. When these white tips were compared with white feathers across 61 other bird species, they were found to reflect 31% more light than the next brightest feather in that dataset (Igic *et al.* 2018; Dunning *et al.* 2023). Hence, they are among the most brilliant white patches measured so far in bird plumages.

fig. 3

Liliana d'Alba

Fig. 3. (a) SEM micrograph of the white retrix tip

transversally cut showing the arrangement of the broadened, overlapping rami resembling Venetian blinds. **(b)** The barbs of the white tail-feather tips contain a disordered network of keratin nanofibres and scattered air pockets, which reflect light in all directions (diffuse reflection).

Acoustic communication during courtship

The vocalisations of the males during roding display flights have been described extensively in the literature (e.g. Glutz von Blotzheim *et al.* 1977; Hirons 1980; Cramp & Simmons 1983; Ferrand & Gossmann 2009), and have been used to distinguish individuals within a population over time (Zimmermann & Santiago 2019). However, less well known are the vocalisations of female Woodcocks, which are scarcely documented. For example, xeno-canto.org holds 1,061 recordings of all woodcock species but just six are labelled as female – two of American Woodcock *S. minor* and four of Eurasian Woodcock. One reason may be that females cannot be readily distinguished in the field, and female responses to male displays are difficult to determine against male vocalisations.

The roding vocalisation of males consists of a a grunting *crôs* (given in *BWP* as *quorr*) call followed by a high-pitched *tsît* (given in *BWP* as *PIETZ*). We found two responses by roding males when they were joined by a second bird. In the first, both birds produced *tsît* calls at irregular intervals, often at the same time, and possibly in vocal competition (fig. 4); while in the second, one bird produced *tsît* calls at regular intervals, while the second bird flew in parallel and gave a *crekk* call in-between the call notes of the male, more akin

to a response (fig. 5). In the first case, we have concluded that the joining bird was a second male, a conclusion backed up by both birds being observed to give typical roding calls (including the *crôs* call) prior to coming together. In the second case, we have concluded that the second bird was a female, since its *crekk* calls appeared to attract roding males (see below). From these findings, we consider that two of the four recordings of Eurasian Woodcock labelled ‘female’ on xeno-canto.org in fact represent males in flight with one another, while one recording is too distorted to be certain. In our opinion, only recording XC636310 (https://xeno-canto.org/636310) represents an interaction between a male and a female.

fig. 4

Fig. 4. Sonogram of two male Eurasian Woodcocks flying together (www.xeno-canto.org/898473). Both produce tsît calls at irregular intervals, often at the same time, and possibly in vocal competition. All vocalisations have been recorded with a Sennheiser ME66 supercardioid microphone, a Sonosax preamplifier followed by a digital recorder (nowadays

Tascam DR-05X); sonograms were edited with the BatSound software.

fig. 5

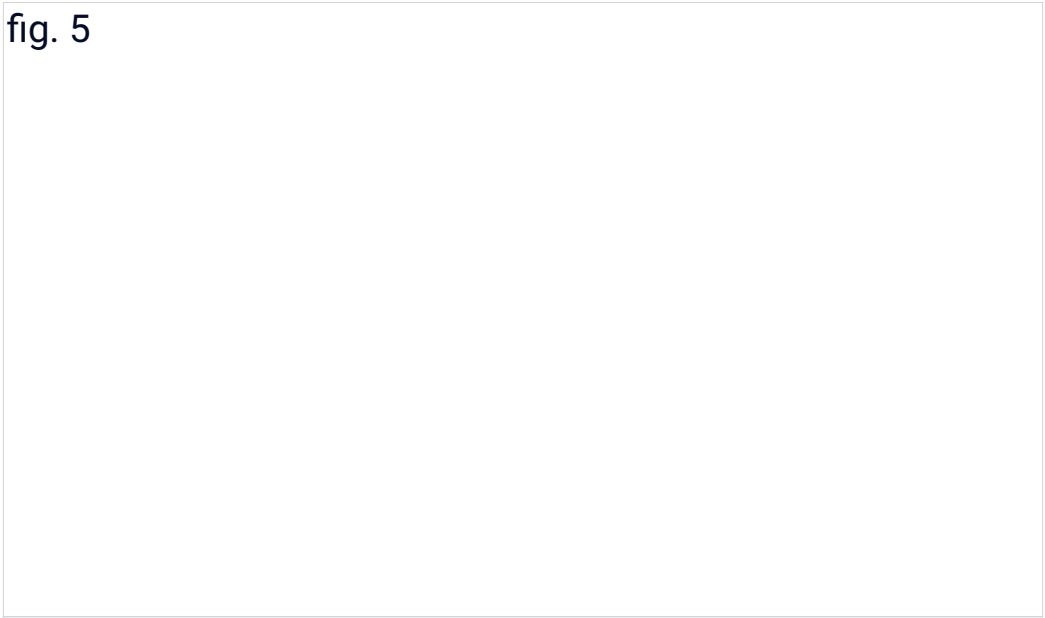


Fig. 5. Sonogram of a male and female Eurasian Woodcock flying in parallel (www.xeno-canto.org/898474). The male gives its normal roding song: the high-pitched tsît (or pssît, 'sneeze-note') (a) is given at regular intervals of about 3.5 s and shows a pair of clear peaks of about 80 ms in length at 4.5 kHz. It is preceded by three low-pitched croaking crôs notes (b). The short, high-pitched crekk call of the female (c) is given at more irregular intervals and shows a less well-defined peak. Compared with the male's tsît call, it is softer and of lower pitch. Females also produce very soft mewing calls (d).

We found that females may produce calls on the ground (fig. 6) as well as when flying at low height (i.e. below the canopy) together with a male. Although these have been described previously (Zedlitz 1927; Haller 1944; Bettmann 1975; Glutz von Blotzheim *et al.* 1977; Cramp & Simmons 1983), it has not been entirely clear to some authors whether females call at all (Ferrand & Gossmann 2009).

fig. 6

Fig. 6. Sonogram of a male uttering its roding song in flight (www.xeno-canto.org/898476); shown at the left are the last four crôs notes followed by a tsît (a) intermingled with ambient noise. A female on the ground gives a crekk call (b) and the male stops singing. The female flies up (c) to join the male in flight and utters several other crekk sounds (d).

Our observations suggest that the *crekk* calls may vary between females, although the small number of available recordings prevents bioacoustic

assessment. Additionally, a male and a female may fly side by side while producing soft mewing calls (fig. 5d), which are difficult to record in the field, or without producing any calls at all.

So far, have not been able to describe with certainty the calls of post-fledging juveniles (i.e. between July and November). However, we expect that their calls may sound much like the *crekk* calls of females.

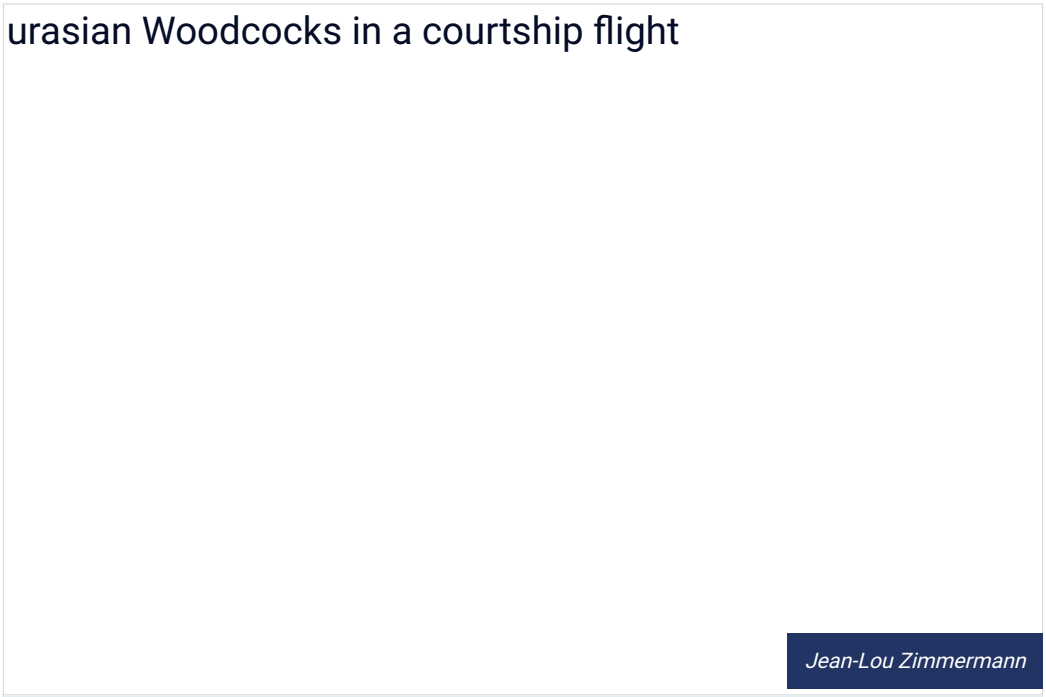
Males, probably in response to females, produce a very high-pitched call and a softer toad-like growling, which is only heard at short distances (figs. 6 & 7). This latter vocalisation has been described previously as dog-like barking (Bettmann 1975; Glutz von Blotzheim *et al.* 1977; Cramp & Simmons 1983; and resembles the sound in the recording XC795044). Several other calls of males and females in various contexts are described in the handbooks by Glutz von Blotzheim *et al.* (1977) and Cramp & Simmons (1983).

fig. 7

Fig. 7. This sonogram shows that the female crekk call can attract males when given from the ground (www.xeno-canto.org/ 898497). The recorded female

call (in blue) is played from a loudspeaker. A male arrives roding and uttering three crôs calls followed by a tsît (a, in green). He stops singing and descends in a parachute-like flight. At about 2 m from the ground, when almost stationary in the air, he utters a very high-pitched, short tsît (b, in green), different from the usual tsît uttered during roding, followed by a long toad-like growling (c, in green). He lands close to the loudspeaker and utters some more growling (not shown) and flies off spontaneously after about four minutes. Another Eurasian Woodcock on the ground utters some tsît calls (in red), but apparently did not interact with the male.

urasian Woodcocks in a courtship flight



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13. Two Eurasian Woodcocks in a courtship flight. They are flying in parallel and produced calls as

described in the main text and shown in fig. 6, indicating they are a male and female.

Combined acoustic and visual communication

Woodcocks remain camouflaged by sitting motionless and silent because the plumage is entirely cryptic from above, with the white tips of the tail feathers hidden. The white tips are only visible from below, so that any functional significance is conditional on raising the tail.

Because of this secretive behaviour in dense vegetation and in low light environments, behavioural observations of Woodcocks on the ground are rare. Hence, it is also difficult to know how visual signals and vocalisations are combined or complement each other. Summaries in Witherby *et al.* (1943), Shorten (1972), Glutz von Blotzheim *et al.* (1977), Cramp & Simmons (1983) and Ferrand & Gossmann (2009), together with our own observations, have shown how visual signals produced by raising and fanning the tail are combined with vocalisations.

The function of roding display flights is to attract the attention of female Woodcocks for mating (e.g. Glutz von Blotzheim *et al.* 1977; Hirons 1980, 1981; Cramp & Simmons 1983; Ferrand & Gossmann 2009). During these roding flights, the white tips of the male's tail are visible to any conspecific on the ground and therefore enhance the conspicuousness of the roding male from below. Males often fan their tail feathers to increase visibility (plate 14a) during lower, butterfly-like flights during the second part of the evening, or after discovering a female on the ground (see below).

Females then probably attract overflying roding males acoustically,

particularly using the *crekk* call, and visually with the tail raised and folded over the back so as to expose the white tips (plate 14b) (Haller 1944; Hagen 1950; Curry-Lindahl 1960; Hirons 1980; Cramp & Simmons 1983; Hirons 1983). To do this, females visit an open space in a wood, where they raise their tail rapidly once or twice in succession and so produce a flash or two which may attract overflying males (Hagen 1950; Ferrand & Gossmann 2009; pers. obs.). Males then approach the female by gliding down in close circles, or more quickly with raised wings, open like a parachute. During descent or on the ground, the male may call with a high-pitched *tsît* or a softer toad-like growling, probably to communicate with another bird (possibly the female) on the ground a short distance away. The female may also produce *crekk* calls when flying with a male (Figs. 5b & 6).

14. Behavioural situations when the white spots at the tip of the tail feathers are visible: (a) flight display by a male; (b) ground display, probably by a female to attract an overflying male; (c) threat display by a male

that was released by placing it on the ground after ringing – it did not fly off but raised the tail before walking away and eventually taking off.

In about 500 instances of playing the female *crekk* call from a loud er, males

roding overhead reacted about one out of every four occasions by changing flight direction, circling around, descending, pausing calling or landing (see also Wadewitz 1977). Similarly, male Woodcocks are attracted by reflective or twinkling objects. Humans have exploited this behaviour for hunting, by fanning Woodcock tails or using reflective or twinkling objects (Fokin & Zverev 2003; Fetisov 2017) to attract roding males; a similar technique was used during the 1970s for catching Woodcocks for conservation research (C. Errington pers. comm.). In the field, we used the reflective surface of a camera flash gun (without triggering the flash) to attract males to land nearby.

When a male lands close to a female, the birds engage in quiet courtship displays on the ground. The female approaches the male with drooping wings and a raised tail. The male circles the female in the same posture with shivering, drooped wings and trembling of the fanned and raised tail (fig. 9; G. J. M. Hirons, V. Marcström and W. Puchalski in Steinfatt 1938; Witherby *et al.* 1943; Ingram 1974; Cramp & Simmons 1983). The tail may also be rapidly fanned to emit a flash of white (Ferrand & Gossmann 2009). The behaviour of a Woodcock that landed close to a nest and raised the tail to give a flash of white observed by des Forges (1975) may also be related to this ground display. It raised its tail and there

fig. 9

Fig. 9. Courtship display of a male and a female Eurasian Woodcock on the ground, both with raised tails (drawing by Friedhelm Weick according to photos by Bruno Hofmann, taken from Glutz von Blotzheim et al. 1977, with permission from U. N. Glutz von Blotzheim).

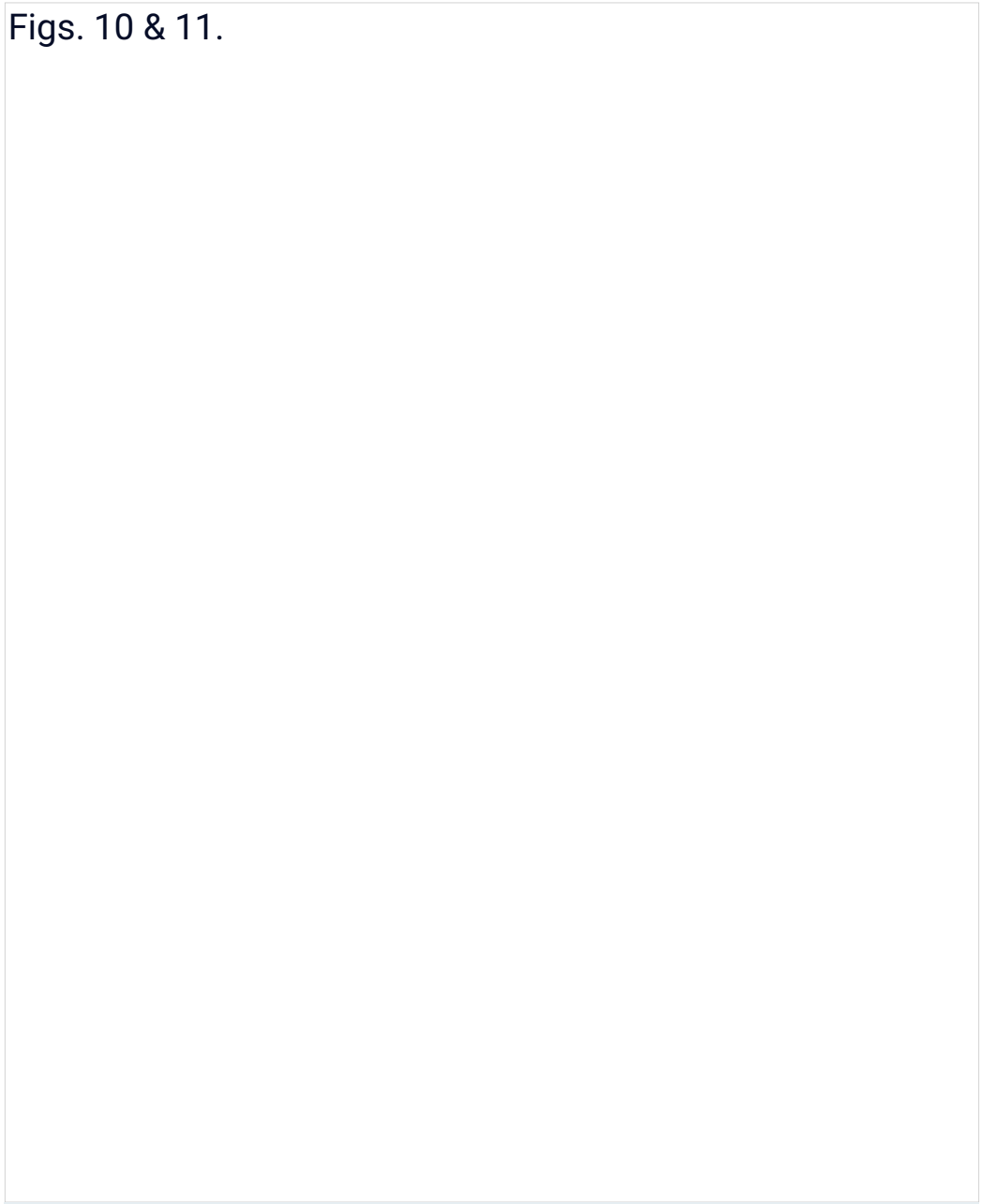
Visual signals are also used in non-breeding situations. Outside the display period, when a Woodcock joins another on the ground, the arriving bird (or both) briefly raises the tail (pers. obs.). Hence, a raised and fanned tail is probably used in intraspecific communication, for example when feeding in fields at night (G. J. M. Hirons in Cramp & Simmons 1983).

Females with young may show distraction behaviours against predators and humans by feigning injury. In short bouts of flight, the legs and tail are dangled (Lowe 1972); on the ground, however, the wings are drooped and the tail is raised (Witherby *et al.* 1943; Ingram 1974; Glutz von Blotzheim *et al.*

1977). Raising the tail and showing the white spots may therefore function to attract the predator to the female and away from the chicks. Raising and fanning of the tail, and lowering of the bill and wings, has also been observed as a display by a female to an unknown intruder (bird or mammal) at the nest (Hosking *et al.* 1980).

Woodcocks may arch the tail and fan it over the back as a threat display when wounded and approached by dogs or humans, when handled for ringing or when trapped (Witherby *et al.* 1943; Williamson 1951; Cramp & Simmons 1983; Ferrand & Gossmann 2009; fig. 9). Additionally, they may also utter various distress calls (figs. 10 & 11).

Figs. 10 & 11.



Figs. 10 & 11. Eurasian Woodcocks (sexes unknown) giving various calls while being handled (https://xeno-canto.org/898482 and https://xeno-canto.org/898483).

Discussion

Although the Eurasian Woodcock is a widespread species that occurs at

considerable densities and is frequently hunted, remarkably little is known about its behaviour, other than the male's roding display. The fact that the sexes are usually not distinguishable in the field hampers assigning their secretive behaviours and vocalisations to males and females. The following discussion is based on our interpretation of the sex roles.

Woodcocks are successively polygynous (Hirons 1981; Cramp & Simmons 1983), i.e. courtship is ongoing during an extended breeding season from March until July/August. Moreover, males with higher roding frequency over woodland have a higher mating success (Hirons 1981, 1983). Thus, male Woodcocks need to continue to display throughout the breeding season, using a combination of vocalisation and visual signals.

Males signal by making roding display flights and vocalisations, and search for females over a large area. This is in contrast to other polygynous species, where males tend to display from a stationary lek and are visited by females (e.g. Ruff *Philomachus pugnax*, Black Grouse *Tetrao tetrix*). Woodcocks call during flight, when out of reach of ground predators. This contrasts with other crepuscular and nocturnal species that call from stationary perches (e.g. owls). Furthermore, the croaking *crôs* calls produced during roding are difficult to locate (Pay in Glutz von Blotzheim *et al.* 1977) and the white tail-tips, directed towards the ground during low and slow roding flights, remain inconspicuous from other angles.

Females remain camouflaged on the ground but may join a male in flight. When on the ground, they produce soft calls and rapid tail-flicking, both of which are perceived at a shorter distance than the roding of males. Hence, female display is limited in terms of its detection, and probably made only in response to male display. Both the flicking of the tail to show the white spots

and the vocalisations on the ground are brief events, specifically directed to a conspecific. Hence conspicuousness in Woodcocks is reduced to a minimum, with the exception of male roding.

As a prey species, the Woodcock has evolved behaviours to distract predators from its chicks, or in response to a predator (or human). For this, they may utter various types of calls and flash their white tail-spots.

The white spots reflect light to an extent unrecorded before in birds. Hence, the white spots might well be an underestimated means of communication in Woodcocks. Remarkably, all eight extant *Scolopax* species show white tail-feather spots with modifications of the rami, while their closest relatives (23 species of non-*Scolopax* Scolopacidae) do not show such white spots (Dunning *et al.* 2023). As far as is known, all *Scolopax* species are crepuscular or nocturnal and inhabit wooded habitats, hence must deal with very dim light conditions. It therefore seems that the genus *Scolopax* has evolved such extremely reflective white spots for visual signalling in the dimly lit wooded environment. Possibly as a consequence, they have been able to reduce vocal communication to very soft sounds when on the ground.

Acknowledgments

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Fig. 1. Eurasian Woodcock *Scolopax rusticola* tail feather shown from above and from below. ***Lukas Jenni and Raffaella Schmid*** [Can 'Normal' be put inverted commas rather than guillemets (x2)? Alternatively, we could just do away with the guillemets. We also need a comma after 'Brownish barbules' top left.]

Fig. 2. Each side of the white spot (left and right of the rachis) on the tip of a Eurasian Woodcock's tail reflects light in different directions. In dim light, only

the side reflecting light directly towards the observer appears brilliant white. Here we show this directionality by illuminating a feather so that light is reflected maximally to the observer from one or the other side. ***Jean-Lou Zimmermann***

Fig. 3. (a) SEM micrograph of the white retrix tip transversally cut showing the arrangement of the broadened, overlapping rami resembling Venetian blinds. **(b)** The barbs of the white tail-feather tips are spongious. They contain many air pockets, which reflect light in all directions (diffuse reflection). ***Liliana d'Alba***.

Fig. 4. Sonogram of two male Eurasian Woodcocks flying together (www.xeno-canto.org/898473). Both produce *tsît* calls at irregular intervals, often at the same time, and possibly in vocal competition. All vocalisations have been recorded with a Sennheiser ME66 supercardioid microphone, a Sonosax preamplifier followed by a digital recorder (nowadays Tascam DR-05X); sonograms were edited with the BatSound software.

Fig. 5. Sonogram of a male and female Eurasian Woodcock flying in parallel

(www.xeno-canto.org/898474). The male gives its normal roding song: the high-pitched “tsît” (or pssît, ‘sneeze-note’) (a) is given at regular intervals of about 3.5 s and shows a pair of clear peaks of about 80 ms in length at 4.5 kHz. It is preceded by three low-pitched croaking *crôs* notes (b). The short, high-pitched *crekk* call of the female (c) is given at more irregular intervals and shows a less well-defined peak. Compared with the male’s *tsît tsit* call, it is softer and of lower pitch. Females also produce very soft mewing calls (d). [Is it possible to delete the caret above the ‘o’ and to change the caret above the ‘i’ to a dot for the text following (a) on the graph?]

Fig. 6. Sonogram of a male uttering its roding song in flight (www.xeno-canto.org/898476); shown at the left are the last four *crôs* notes followed by a *tsît* (a) intermingled with ambient noise. A female on the ground gives a *crekk* call (b) and the male stops singing. The female flies up (c) to join the male in flight and utters several other *crekk* sounds (d).

Fig. 7. This sonogram shows that the female *crekk* call can attract males

when given from the ground (www.xeno-canto.org/898497). The recorded female call (in blue) is played from a loudspeaker. A male arrives roding and uttering three *crôs* calls followed by a *tsît* (a, in green). He stops singing and descends in a parachute-like flight. At about 2 m from the ground, when almost stationary in the air, he utters a very high-pitched, short *tsît* (b, in green), different from the usual *tsît* uttered during roding, followed by a long toad-like growling (c, in green). He lands close to the loudspeaker and utters some more growling (not shown) and flies off spontaneously after about four minutes. Another Eurasian Woodcock on the ground utters some *tsît* calls (in red), but apparently did not interact with the male.

Fig. 8. Response of a male Eurasian Woodcock to female sounds played from a loudspeaker (www.xeno-canto.org/898481). In the sonogram, the recorded female call is played at regular intervals (some labelled 'a'); an arriving, roding male utters a last *tsît* (b) before he stops singing and lands (c) on a trunk on the ground at about 3 m from the loudspeaker. He looks around, possibly searching for a visual signal, and utters two very loud, high-pitched *tsît* notes (d, e), different from the usual *tsît* calls uttered during roding. Another male flies over give his roding song (f, g). The first male flies off (h) and joins the second male in flight.

Fig. 9. Courtship display of a male and a female on the ground, both with raised tails (drawing by Friedhelm Weick according to photos by Bruno Hofmann, taken from Glutz von Blotzheim *et al.* 1977, with permission from U. N. Glutz von Blotzheim).

Figs. 10 & 11. Eurasian Woodcocks (sexed unknown) giving various calls while being handled (https://xeno-canto.org/898482 and https://xeno-canto.org/898483).

001 & 002. The two sides of the white spot on the tip of the tail of Eurasian Woodcocks *Scolopax rusticola* reflect light in different directions. Hence, in dim light, only the side reflecting light towards the observer appears brilliant white, as shown on most of the tail feathers of the flying bird and on the three outermost rectrices on the part of the tail highlighted on the sitting bird (see also fig. 2). ***Jean-Lou Zimmermann***

003. Two Eurasian Woodcocks in a courtship flight. They are flying in parallel and produced calls as described in the main text and shown in fig. 6, indicating they are a male and female. ***Jean-Lou Zimmermann***

004. Behavioural situations when the white spots at the tip of the tail feathers are visible: **(a)** flight display by a male ***Jean-Lou Zimmermann***; **(b)** ground display, probably by a female to attract an overflying male ***Serge Santiago***; **(c)** threat display by a male that was released by placing it on the ground after ringing – it did not fly off but raised the tail before walking away and eventually taking off. ***Jean-Lou Zimmermann***

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