Attraction of kestrels to vole scent marks visible in ultraviolet light

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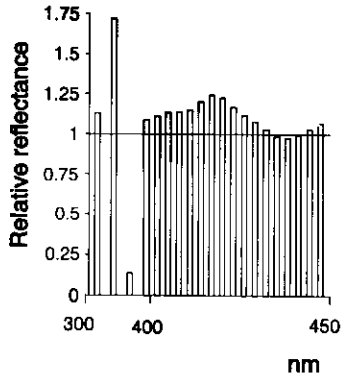

FIG. 1 Reflection of scent marks of a male field vole on cardboard used in a laboratory experiment, relative to clean cardboard. A value of 1 represents clean cardboard (horizontal line), values <1 denote greater absorption and those >1 greater reflection than clean cardboard. Each column is a mean of five measurements (Spectroradiometer SR-500). The bandwidth in visible light was 3 nm but the UV filters penetrated a 10-nm band. At visible wavelengths, the reflection remained close to 1 up to 690 nm. The figure shows that there are contrasts in UV wavelengths that facilitate the detection of vole scent marks by a UV-sensitive spectator. There is a clear absorption at 370 nm (in the UV wavelength range of the laboratory experiment). The clean cardboard also reflected UV light considerably, so the reflection peak near 340 nm may also be visible in the wild in UV-absorbing green vegetation.

Attraction of kestrels to vole scent marks visible in ultraviolet light

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In northern Europe, broad four-year oscillations in small rodent and raptor populations are synchronous over hundreds of square kilometres[1–6]. Crashes in vole populations can induce wide emigration (>1,000 km) of their predators[7–9], but almost nothing is known about how predators rapidly detect areas of vole abundance. Here we report on laboratory and field experiments on voles (*Microtus agrestis*) and kestrels (*Falco tinnunculus*). Voles mark their runaways with urine and faeces, which are visible in ultraviolet light. Wild kestrels brought into captivity were able to detect vole scent marks in ultraviolet light but not in visible light. In the field, kestrels hunted preferentially near experimental nest-boxes where artificial trails were treated with vole urine and faeces. We suggest that kestrels flying over an area can see and use vole scent marks to assess vole numbers. This ability would enable kestrels to 'screen' large areas in a relatively short time. Our results provide a novel explanation for how raptors detect patches of high vole densities without prior knowledge of local food resources.

The Eurasian kestrel (*Falco tinnunculus*) (hereafter kestrel) is a widespread, open-country raptor that is migratory in Fennoscandia. Kestrels detect prey visually, feeding primarily on small mammals that they capture on the ground[10]. Their main hunting modes are wind-hovering, soaring and perching[10]. Small rodents mark their runaways with urine and faeces[11,12]. These marks are visible in ultraviolet light (wavelengths of 320–400 nm)[13] (Fig. 1). The above-ground runaways of voles are clearly visible to raptors, especially in spring. Their bottoms (3–4 cm wide) are soaked by urine and faeces. We tested the hypothesis that kestrels use vole scent marks visible in ultraviolet light as a cue for discovering prey patches in laboratory and field experiments.

For the laboratory investigation we used a room measuring 5 × 4 × 2.5 m at the Konnevesi Research Station, with the walls covered by black paper to exclude other visible cues for orientation. There was no natural light in the room. Kestrels were observed from a dark hide through a 30 × 30-cm wire-mesh window with 1 mm openings so that the observer was invisible. This experimental situation was not unnatural, as wild kestrels sometimes hunt inside small barns.

In the laboratory experiment, captured wild kestrels were each given a choice of four adjacent identical arenas: arena in ultraviolet light with vole trails, clean arena in ultraviolet light, vole trail arena in visible light, and clean arena in visible light (Fig. 2). In terms of both the time spent above the arenas and the number of scans, kestrels preferred the vole-trail arena illuminated by ultraviolet light over other arenas, whereas the clean arena illuminated by ultraviolet light was less favoured than any other (Fig. 2); there was no difference in preference between the two arenas illuminated by visible light. We propose that kestrels found the vole-trail arena in ultraviolet light more interesting than the clean arena under the same lighting conditions because they could see fresh signs of voles in the former. Their interest in the two arenas in visible light was intermediate, possibly because they could not discern whether these arenas contained signs of voles.

The field experiment was conducted in the Alajoki study area (63° N, 23° E), which is a large (100 km^2) tract of level farmland in western Finland. Because most fields are ploughed in autumn, the only habitat suitable for voles during winter and early spring is along ditches[14]. Kestrels can breed in nest-boxes fastened on barns and individual trees[5]. They are highly nomadic, as shown by a mean turnover of 75% for males and 92% for females during the breeding seasons of 1983 to 1992 (ref. 15). Annual breeding densities of kestrels at Alajoki vary from 4 to 98 nests per 100 km^2 and synchronously with vole densities[5,6].

In spring 1993, vole densities at Alajoki were extremely low, so no vole trails (runaways) were evident. In early April (before the arrival of kestrels), we chose 45 kestrel nest-boxes (in an area of 15 km^2) and randomly placed them into one of three

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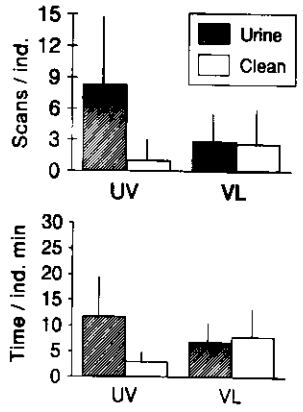

FIG. 2 Mean time (min, +s.d.) spent by the 19 kestrels above four adjacent 1 × 2 m arenas (below) and mean number of scans (+s.d.) of the falcons on different arenas (top). The four options were: dry vole trails (urine and faeces) in UV light, clean (no vole trails) arena in UV light, dry vole trails (urine and faeces) in visible light (VL) and clean arena in visible light (VL). Vole trail arenas had been occupied by seven field voles for 17 hours before the experiment and two had been without voles. The voles were removed before introducing kestrels to the arenas. Two 160-W black-light UV bulbs (Philips MLW 160W; spectral energy distribution shown in Fig. 4*a*) illuminated one arena of each group. The intensity of UV (320–400 nm) on the arena floor below the lamps varied from 0.016 to 0.025 mW cm^{-2}. Two ordinary 60-W bulbs (OSRAM 9W3, 60W; irradiance spectrum shown in Fig. 4*b*) emitting <1% UV illuminated the other arenas. The sockets of the lamps were 115 cm above the bottom of the arenas. The intensity of VL (400–700 nm) on the arena floor below the lamps varied from 0.55 to 0.67 mW cm^{-2}. The temperature difference on the bottom of the arenas between UV and VL treatments was <0.2 °C. On UV arenas there also was some VL scattered from the lamps above the VL arenas. It was enough to mask possible fluorescence and to facilitate recording of falcon behaviour. There was also UV scattering on VL arenas, but our gauge was not sensitive enough to measure it. Each arena had a hard brown cardboard floor and identical nest-box for voles. Arena positions were changed after each exposure. There was a perch for kestrels above each arena. Nineteen kestrels (8 young of the year (age 6–8 weeks) and 11 adults), starved on the day before the experiment, were individually introduced to the experimental room twice for 15 min each time. The time between introductions of a falcon was at least 48 h. The time spent above each arena was recorded, as was the number of scans by each falcon; that is, the times when the kestrel pointed its eyes to an arena, bobbing its head to estimate the distance to the target, an easily discernible hunting mode of the kestrel[10]. The means of the distributions were compared after square-root transformation by SPSS/two-way ANOVA for repeated measures (d.f. = 1, 18). For time spent above the arenas, the effect of light was nearly significant ($F = 3.13$, 2-tailed $P = 0.095$) and the effect of vole scent marks highly significant ($F = 32.04$, $P < 0.001$; interaction term $F = 15.95$, $P = 0.001$). For the number of scans, the effect of light was not significant ($F = 0.24$, $P = 0.63$), whereas the effect of scent marks was significant ($F = 10.42$, $P = 0.005$; interaction term $F = 18.09$, $P = 0.001$). The contrasted differences between arenas in UV light with and without scent marks were: $F = 31.86$, $P < 0.001$ for time spent and $F = 44.44$, $P < 0.001$ for the number of scans, and between arenas in VL with and without scent marks: $F = 0.56$, $P = 0.47$ for time spent and $F = 0.20$, $P = 0.66$ for the numbers of scans.

experimental categories: (1) artificial vole trails with urine and faeces; (2) artificial vole trails without urine and faeces; and (3) no vole trails (control) (Fig. 3*a*). We counted raptors near the boxes during 24 mornings using binoculars and a telescope. Each nest-box was observed for 15–30 min each morning for a total of 6–7 hours. During observation periods, we recorded the species, sex and behaviour (hunting (hovering, soaring and perched-hunting), paired (both sexes near box) or resting) of all raptors seen near the boxes. It is fairly obvious when a kestrel is hunting from a perch, because it has an upright posture, continually bobs its head and scans the ground, and often alters perch[10]. All these behaviours are different from those of resting kestrels, which sit hunched up with feathers fluffed out, or preen. Because the study area consisted mostly of open agricultural fields (73%), we detected most (if not all) of the raptors present during observation periods.

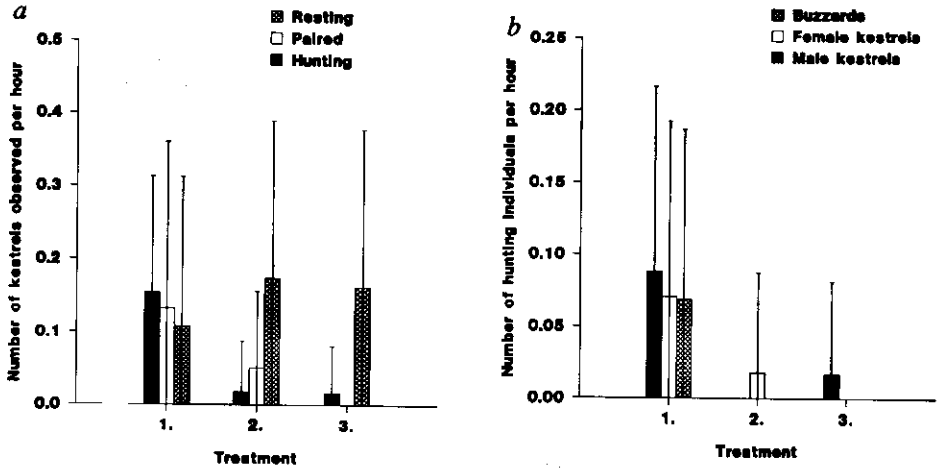

FIG. 3 *a*, Log-transformed (log(n+1)) number of hunting, paired and resting kestrels observed per hour near nest-boxes. Boxes were randomly assigned to one of three experimental treatments (15 boxes per treatment), and the bars show the mean (+s.d.) number of kestrels per box. In treatment 1, we created four artificial vole runaways in ditches within 100 m of each nest-box by cutting grass on four 10-m long and 4–6-cm wide trails. Trails were treated with straw taken from cages that had contained field voles held over the previous winter at the Konnevesi Research Station, so the straw was saturated with vole urine and faeces. In treatment 2, artificial vole trails were created at each nest-box as in treatment 1, except trails were treated with straw taken from surrounding fields and wetted with water from nearby ditches. Water blended with vole urine and faeces (treatment 1) or taken from ditches (treatment 2) was added to the trails once a week over 5 weeks. Nest-boxes assigned to treatment 3 served as controls, for which no vole trails, or urine and faeces or water treatments were made. ANOVA indicated that the log-transformed number of hunting ($F_{2,42} = 8.36$, 2-tailed $P = 0.001$) and paired ($F_{2,42} = 3.23$, $P = 0.049$) kestrels differed among treatments, whereas the number of resting kestrels was equal among treatments ($F_{2,42} = 0.41$, $P = 0.67$). In general, hunting kestrels came preferentially near boxes containing artificial trails treated with vole urine and faeces (Tukey test for the difference between treatments 1 and 2, 2-tailed $P = 0.003$; between treatments 1 and 3, $P = 0.003$). *b*, Log-transformed (log(n+1)) mean (+s.d.) number of hunting male kestrels, female kestrels and rough-legged buzzards observed per hour near nest-boxes, classified by experimental treatments as outlined in *a* (1 represents artificial vole trails treated with straw and vole urine and faeces; 2, artificial vole trails treated with straw and water; and 3, control). The log-transformed number of male kestrels (ANOVA, $F_{2,42} = 4.72$, $P = 0.014$) and the number of rough-legged buzzards (Kruskall–Wallis test, $H = 8.56$, $P = 0.014$) differed significantly among treatments, whereas the log-transformed number of female kestrels approached significance ($F_{2,42} = 3.11$, $P = 0.055$). Male kestrels hunted more frequently near nest-boxes that had artificial trails treated with vole urine and faeces (Tukey–test for the difference between the treatments 1 and 2, 2-tailed $P = 0.016$; between the treatments 1 and 3, $P = 0.06$).

Kestrels were observed near 27 experimental nest-boxes. They hunted preferentially near nest-boxes where artificial trails had been created using vole urine and faeces (Fig. 3*a*). In contrast, hunting kestrels largely avoided areas near boxes with trails but no urine and faeces, or with no trails (Fig. 3*a*). Thus, kestrels were not using the trails themselves as cues for hunting. Paired kestrels also tended to occupy boxes near trails treated with vole urine and faeces, whereas resting kestrels chose boxes irrespective of treatment (Fig. 3*a*). Male kestrels provide for their mates from pair formation onwards, during which time females do not hunt but remain near their nest-box in preparation for egg-laying[10,16]. Therefore, the number of male kestrels hunting near boxes was greater than the number of females. This may explain why treatments differed in the number of hunting kestrels, significantly for males (which preferred to hunt near urine- and faeces-treated trails) but only marginally for females (Fig. 3*b*). In addition, the four rough-legged buzzards (*Buteo lagopus*) seen hunting near nest-boxes were all near sites treated with vole urine and faeces (Fig. 3*b*).

We have provided the first experimental evidence, to our knowledge, of a wild raptor using vole trail marks to select hunting patches and potential nest-sites. We suggest that scent marks of voles act as visible cues to kestrels, especially in spring when these are not covered by grass. In the laboratory experiment, we did not detect any peak of visible light in the ultraviolet arenas that might explain our results (Fig. 4). It is known that mouse urine fluoresces in blue[13], and we have found a dim blue fluorescence in the urine and faeces of voles. It is possible that the ability of kestrels to detect vole scent marks may not depend entirely on ultraviolet vision. The faint fluorescence is just visible to a human spectator when ultraviolet lamps are the only source of light: light from ordinary 60 W bulbs masks it completely. At Alajoki during our field experiment, the visible sunlight was so strong that any fluorescence was totally masked; we therefore consider it unlikely that fluorescence was the reason for our results. An alternative explanation, that kestrels detect vole scent marks by olfaction, is also unlikely, as in our laboratory experiment kestrels were able to distinguish vole scent marks in ultraviolet but not visible light. The biological significance of ultraviolet vision in higher vertebrates is poorly understood: it may play a role in orientation[17,18], food detection[19,20] and intraspecies communication[21,22] (reviewed in refs 23, 24). The absorbance or reflection of ultraviolet light by a food item could make it more conspicuous to a consumer. Although the eye structure of diurnal raptors (order Falconiformes) has not been tested systematically for sensitivity to ultraviolet light, most other diurnal birds studied so far have proved to be sensitive[24–26]. We therefore propose that, in the presence of ultraviolet light, diurnal raptors can easily see areas stained with fresh vole urine and faeces, and that they use these marks as visual cues when searching for areas of vole abundance. This ability would enable raptors to evaluate large areas in a relatively short time and would explain how nomadic raptors find patches of high vole abundance without prior knowledge of local food conditions. It has been suggested that scent marks of other vertebrates may also be visible in ultraviolet light[27], so this kind of hunting-site detection may not be uncommon. □

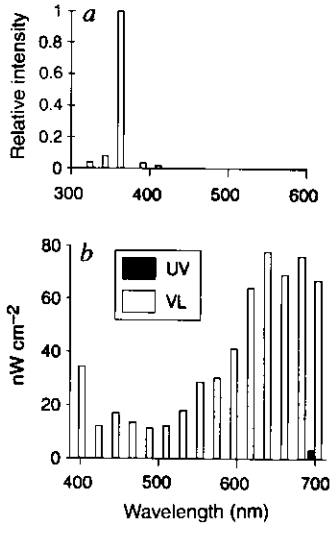

FIG. 4 *a*, Relative spectral energy distribution of the UV lamp (Philips MLW 160 W, 220–240 V) according to the manufacturer. *b*, The irradiance spectra between 400 and 700 nm on the bottom of UV arenas (UV) and visible light (VL) arenas measured with a series of interference filters (each penetrating ~15-nm band) immediately below the UV and VL lamps, respectively. The small amount of VL emitted by UV lamps (410 nm in *a*) was not measurable using our gauge.

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