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Combining radio-telemetry with direct observations, we followed 22 released juvenile captive-bred capercaillies throughout the day to assess if their seasonal and daily patterns of activity, movements, and diet are in accordance with published information on wild birds. Day length was the most important factor determining birds' mobility and activity. Capercaillies were active for $46 \pm 2\%$ of daytime, during which they mostly foraged ($30 \pm 2\%$). The average distance travelled per day was 0.93 ± 0.14 km. The time budget of capercaillies was mostly allocated to activities on the ground but they spent at least 20% of the daytime in trees. They fed primarily on blueberries, cowberries and pine needles. The mean daily feeding time in fall and winter was 3 h, but it increased to 6 h in spring and summer. We conclude that released birds behave similarly to wild birds and reintroduction of captive-bred capercaillies can be successful if the initial mortality is reduced.

Populations of capercaillie *Tetrao urogallus* have declined throughout central and western Europe over the last decades. Although the species is not considered to be threatened over its total range, many local populations in this region have become extinct, while remaining small and isolated populations are threatened (Storch 2007). The most frequently reported threats for capercaillie populations are habitat loss and fragmentation (Klaus 1991, Kurki et al. 2000, Saniga 2003), the effects of predators (Kurki et al. 1997, Baines et al. 2004, Åhlén et al. 2013), weather conditions (Moss et al. 2001), hunting and human disturbance (Thiel et al. 2007, 2011, Storch 2013) and genetic isolation (Segelbacher et al. 2003). Although each of these factors can increase mortality of capercaillies, there is no clear evidence which factor caused the general decrease in such a large and ecologically diverse area.

The release of birds reared in captivity is the most common method in attempts to re-establish extinct populations of capercaillies (Klaus 1998, Seiler et al. 2000). Several thousand captive-reared birds have been released since the 1950s in central Europe (Klaus and Bergmann 1994, Seiler et al. 2000, Siano and Klaus 2013), but there is no evidence of successful restorations (Storch 2007, Siano and Klaus 2013). Reintroduction failure is largely a result of high predation

rates, which are often explained by morphological, physiological and behavioural deficits of released birds caused by captive breeding (Liukkonen-Anttila et al. 2000, Siano et al. 2006). Re-establishment of self-sustaining wild populations requires that conservationists know if captive-reared birds will behave naturally once released.

In the early 1960s, the population of capercaillies in the Lower Silesia Forest was the largest in Poland, estimated at 360 birds (Buła 1969), but by 2009 only two birds remained (Merta et al. 2013). Therefore, the Ruszów Forest District decided to launch a restocking programme.

In this paper, we present a data set of 139 days of continuous radio-tracking combined with direct observations obtained among 22 capercaillies released into the Lower Silesia Forest, Poland. The aim of the study was to quantify activity patterns, movements and diet and compare them to those of wild birds.

Study area and methods

The study area is located in the Lower Silesia Forest (51°21′N, 150°7′E), a continuous lowland (140–180 m a.s.l.) forest area covering 2500 km². The forest is commercially exploited and dominated by even-aged stands of Scots pine *Pinus sylvestris*, constituting 93% of the forest. Pine stands are supplemented by birch *Betula pendula*, spruce *Picea abies*, oak *Quercus robur* and beech *Fagus sylvatica* (Kobielski et al. 2007). The forest undergrowth consists of blueberry

Vaccinium myrtillus, cowberry *V. vitis-idaea*, heather *Calluna vulgaris*, wild rosemary *Ledum palustre* and swamp cranberry *Oxycoccus palustris*. Red fox *Vulpes vulpes*, pine marten *Martes martes*, raccoon dog *Nyctereutes procyonoides*, raccoon *Procyon lotor* and northern goshawk *Accipter gentilis* are potential predators of capercaillies in the study area.

The climate is temperate, with an annual mean temperature of 8.3°C and an average annual precipitation of 550 mm. The mild winters last on average for 70 days, with approximately 40 days of snow cover, an average temperature of –2°C and an average precipitation of 45 mm in January. The growing season (temperature over 5°C) lasts for 220 days. The mean temperature is 18°C in July, when there is also the highest rainfall (100 mm).

In 2010–2013, we released a total of 98 juvenile capercaillies at the age of 16 weeks (Merta et al. 2015). We fitted 22 of released birds (mean mass males = 3.2 kg, SD = 0.2 kg, n = 16; females = 1.8 kg, SD = 0.1 kg, n = 6) with back-pack VHF radio-transmitters lasting for 42 months (33 g, which was about 1% of body mass of males and 2% of females) and equipped with mortality sensors (Biotrack Ltd). We monitored daily activity and behaviour of radioed birds by a combination of radio-tracking and visual observations for a total of 139 full days. The age of monitored birds ranged between 131 and 1211 days post-hatch. They originated from two breeding centres that used different methods of rearing and were released by two different methods (Merta et al. 2015). Sixteen of the radio-tracked birds were reared in 'semi-liberty' by their captive mother and released next to the cage of their mother (Krzywiński et al. 2013). Six chicks were reared in captivity and released in the absence of their mother, and this group suffered a higher mortality rate (Merta et al. 2015).

Once a month, we monitored each bird for an entire day. A team of two observers located the roosting site of a radio-tracked bird before sunrise by homing-in with radio-telemetry. The observers remained 10–60 m away from the bird, which allowed them to observe the bird with binoculars (10 × 50) and followed it throughout the day until it roosted again after sunset. Usually, we were able to follow birds continuously. However, when birds flew off, observers re-located them by radio-telemetry. We did not include the time while birds were lost in the analyses, but this consisted only of 3% of observation time (48 of 1649 hours). We recorded time and type of behaviour (resting, feeding, moving, flying, preening), type of food, GPS location and, if the bird was on a tree, its height and the species of tree. We identified the plant species that the birds consumed, but did not specify which part of the plant was consumed. When we were not able to identify the species, we excluded the observation from the diet analysis (121 of 2447 cases). We estimated the daily range as the 100% minimum convex polygon (MCP) of all locations of a given day, as recommended by Gula and Theuerkauf (2013). As the birds originated from captive breeding, they were more habituated to humans than wild birds and they generally accepted the observers in a relatively close distance. However, whenever we noticed that the bird fled when approached, we stopped the observations and excluded the day from the data analyses. Birds were continuously vigilant during the observations. Therefore, we did not specify vigilance as a distinctive behavioural category.

We assessed daily patterns of activity, movements and feeding by averaging the proportion of time of a particular behaviour for every hour of the day. We tested using general linear models (GLM) with IBM SPSS Statistics 22 if 1) age of birds, 2) sex, 3) breeding method and 4) day length influenced daily ranges, distance travelled per hour and number of times capercaillies fed per h. We then chose the regression model that best fit the data to represent relations between dependent variables and factors presented in the figures. As we noticed that some relations were different in winter (day length < 12 h) and in summer (day length > 12 h), we used separate regression lines. All means are presented with 95% confidence intervals.

Results

The daily ranges of capercaillies varied with day length (GLM, DF = 138, F = 4.568, p = 0.034), but not with age (F = 2.492, p = 0.117), breeding method (F = 0.213, p = 0.645), or sex (F = 0.041, p = 0.839). The average daily range of capercaillies was 0.076 ± 0.026 km² and increased exponentially with increasing day length (Fig. 1A).

The number of feeding bouts per h varied with day length (GLM, DF = 138, F = 4.751, p = 0.031), but not with age (F = 0.090, p = 0.765), breeding method (F = 1.009, p = 0.317), or sex (F = 0.205, p = 0.652). We therefore pooled all individuals of different age, sex and rearing method for further analyses. Capercaillies left the night
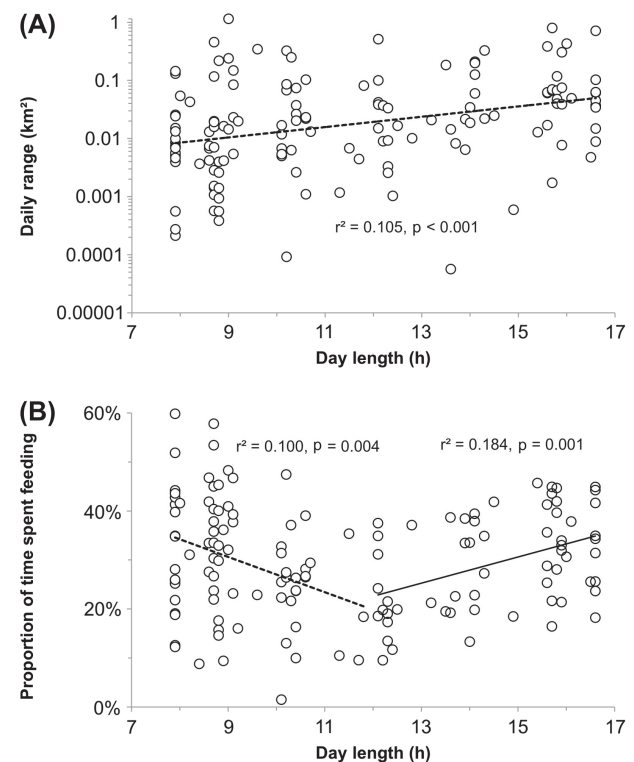

Figure 1. (A) exponential relation (dotted line) between day length and daily range (logarithmic scale), and (B) linear relations between day length and proportion of day spent feeding for winter (dotted line) and summer (continuous line) separately of 22 young capercaillies radio-tracked for 139 full days.
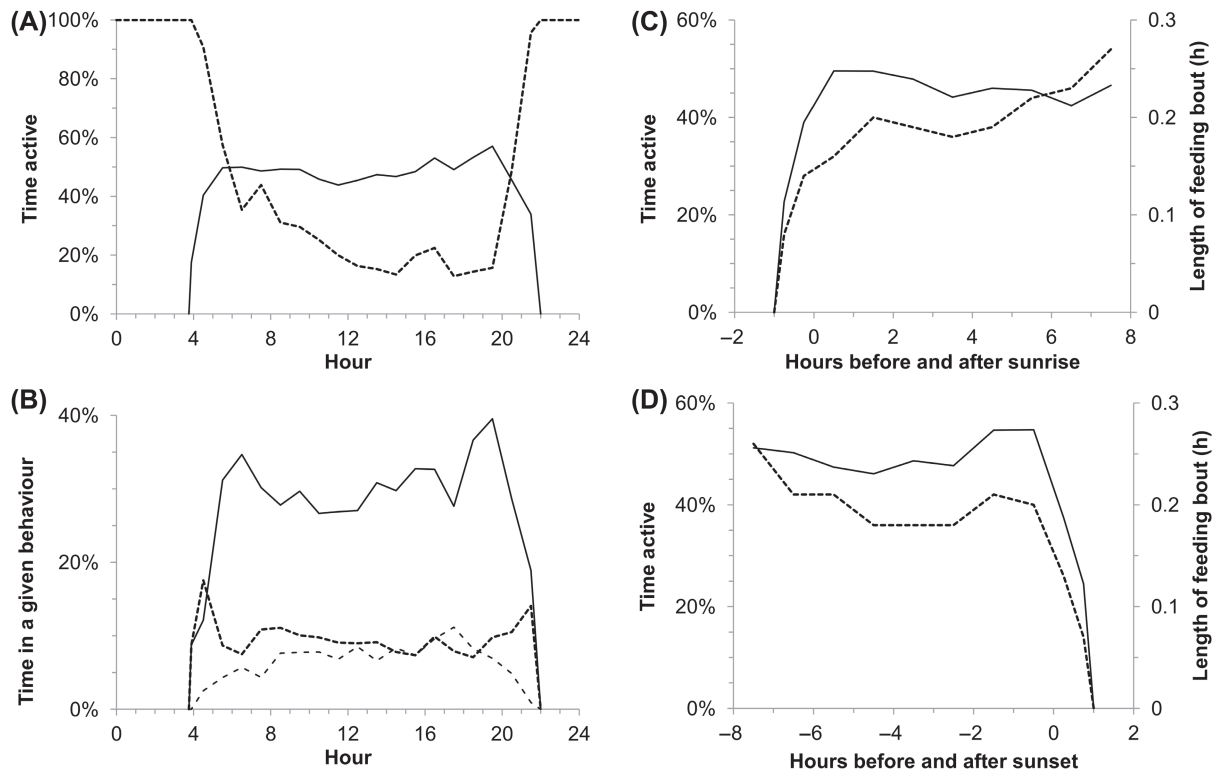
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Figure 2. Daily patterns of (A) time active (continuous line) and time spent in trees (dotted line), (B) time spent feeding (continuous line), time spent preening (dotted line) and time spent moving or flying (dashed line), (C) time active (continuous line) and average length of feeding bout (dotted line) in relation to sunrise and (D) time active (continuous line) and average length of feeding bout (dotted line) in relation to sunset of 22 capercaillies radio-tracked for 139 full days. For clearness of the figures, we did not present confidence intervals.

roost on average 14 ± 7 min before sunrise (range: 48 min before to 34 min after sunrise, n = 30) and started perching at the night roost on average 11 ± 3 min after sunset (range: 75 min before to 55 min after sunset, n = 140). They roosted mainly in branches of pine trees (159 of 162 nights) at a mean height of 13 ± 1 m. We only recorded once a capercaillie roosting on the ground.

Capercaillies were active $46 \pm 2\%$ of daytime with a small peak during the two hours before sunset (Fig. 2A). Most of their time budget was allocated to activity on the ground but they spent at least 20% of time in trees at any hour of

the day (Fig. 2A). Both feeding and preening patterns had distinctive peaks during the crepuscular periods of the day (Fig. 2B). Capercaillies moved throughout the day after the morning feeding peak, but movements were highest just before the evening feeding peak. The timing of activity was mainly related to sunrise and sunset (Fig. 2C–D).

Feeding was the main activity of capercaillies during the day (Table 1). Feeding time increased from 3 h to almost 6 h per day from spring to summer (Fig. 3A, 1B). In fall and winter feeding time was relatively stable at about 3 h, but the proportion of time spent feeding was inversely related to the

Table 1. Averages (with 95% confidence intervals) of daily range, movements and activity of 22 (6 females and 16 males) radio-tracked young capercaillies (n = 139 days) from 2010 to 2013 in the Lower Silesia Forest, Poland.

|	Summer		Winter	
	Females (n = 7)	Males (n = 53)	Females (n = 15)	Males (n = 64)
Daily range (km²)	0.022 ± 0.019	0.108 ± 0.048	0.031 ± 0.031	0.066 ± 0.42
Distance travelled per h (km)	0.055 ± 0.020	0.078 ± 0.016	0.068 ± 0.038	0.086 ± 0.021
Distance travelled per day (km)	0.81 ± 0.32	1.16 ± 0.23	0.65 ± 0.37	0.82 ± 0.20
Number of feeding bouts per h	1.7 ± 0.3	1.4 ± 0.1	1.8 ± 0.4	1.7 ± 0.2
Length of feeding bout (h)	0.20 ± 0.05	0.21 ± 0.02	0.22 ± 0.05	0.18 ± 0.02
Time foraging per day (h)	5.1 ± 1.7	4.5 ± 0.5	3.2 ± 0.6	2.7 ± 0.3
Proportion of day spent				
foraging	$34.4 \pm 7.2\%$	$28.9 \pm 2.8\%$	$35.7 \pm 6.9\%$	$28.8 \pm 3.0\%$
moving	$7.4 \pm 3.1\%$	$7.6 \pm 1.8\%$	$6.5 \pm 3.0\%$	$6.4 \pm 1.8\%$
flying	$0.4 \pm 0.5\%$	$0.3 \pm 0.2\%$	$0.8 \pm 0.4\%$	$0.8 \pm 0.2\%$
preening	$9.0 \pm 1.7\%$	$9.8 \pm 1.3\%$	$5.9 \pm 3.1\%$	$8.8 \pm 1.3\%$
not active	$49.1 \pm 8.6\%$	$53.3 \pm 3.4\%$	$51.2 \pm 6.6\%$	$55.2 \pm 3.9\%$

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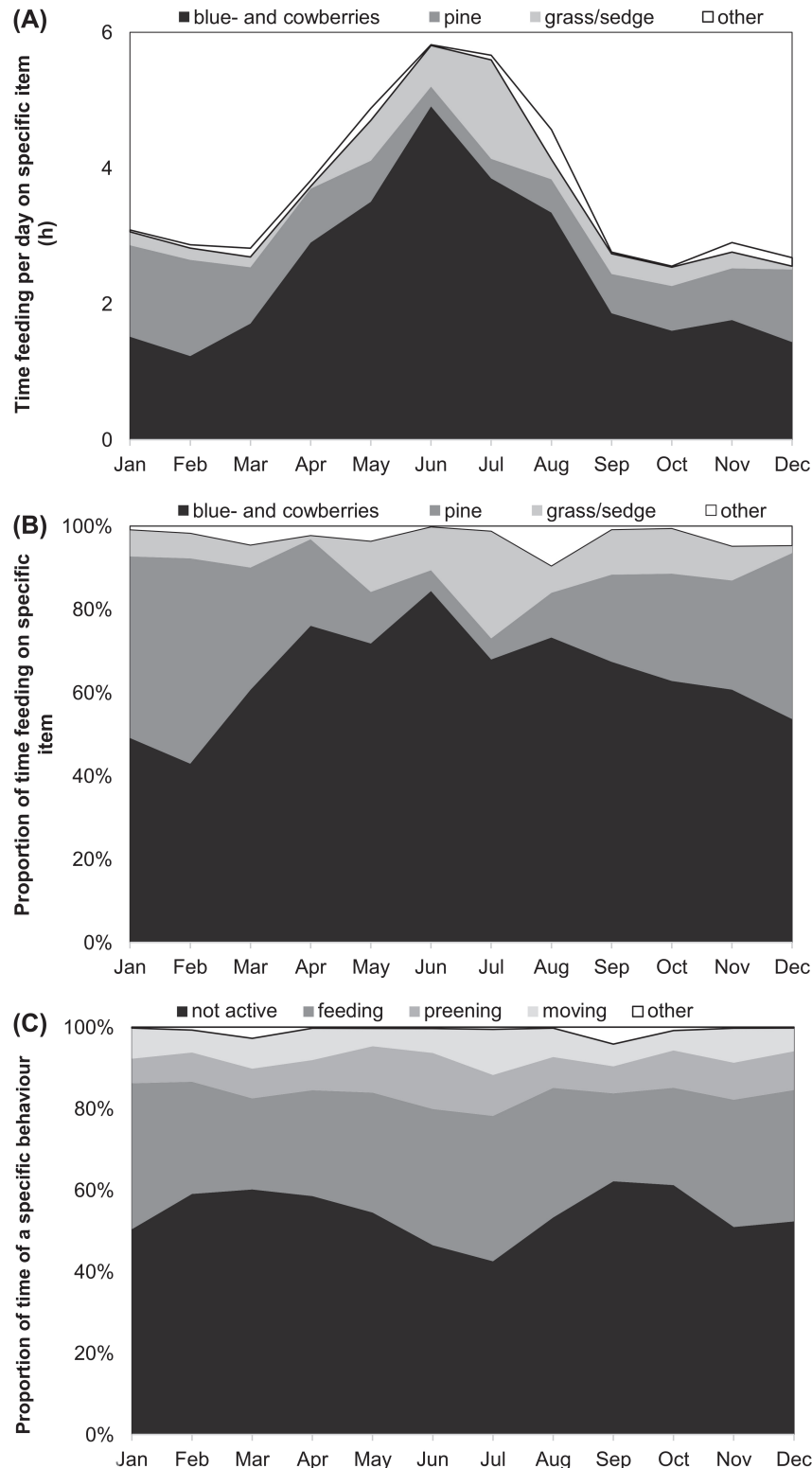
Figure 3. Annual variation in (A) total time of day spent feeding on major food items, (B) proportion of time spent feeding on major food items, and (C) average proportion of time spent not active, feeding, preening, moving (including flying) or in another activity of 22 young capercaillies radio-tracked for 139 full days.

day length (Fig. 1B). The average feeding bout lasted 12 ± 1 min but the length depended on the food item (Table 2).

Distance travelled per h (0.08 ± 0.01 km, range = 0.003 to 0.4 km) varied with age (GLM, DF = 138, F = 5.607,

$p = 0.019$), but not with day length (F = 0.212, $p = 0.646$), breeding method (F = 2.090, $p = 0.151$), or sex (F = 0.005, $p = 0.945$). Distance travelled per day (0.93 ± 0.14 km, range = 0.04 to 3.8 km) also varied with age (GLM,

Table 2. Identified food items (n = 2326, additional 121 cases for which we could not identify the item excluded) and average time per feeding bout of a specific item (with 95% confidence intervals) for 22 radio-tracked young capercaillies observed over 139 full days.

Item	No. of times eaten	Feeding bout (min)
Blue- and cowberry (*Vaccinium myrtillus, V. vitis-idaea*)	1267	14 ± 1
Scots pine (*Pinus sylvestris*)	688	9 ± 1
Grass/sedge (*Poaceae/Carex* spp.)	254	10 ± 1
Spruce (*Picea abies*)	50	6 ± 1
Heather (*Calluna vulgaris*)	38	11 ± 3
Bracken (*Pteridium aquilinum*)	9	4 ± 1
Supplemental food (*Avena sativa, Triticum aestivum, Zea mays*)	4	8 ± 7
Meadowsweet (*Spiraea tomentosa*)	4	8 ± 5
Wild rosemary (*Ledum palustre*)	4	7 ± 6
Larch (*Larix decidua*)	3	5 ± 0
Oak (*Quercus robur*)	2	5 ± 3
Rasp- and blackberry (*Rubus idaeus, R. fruticosus*)	2	3 ± 2
Birch (*Betula pendula*)	1	9

DF = 138, F = 4.402, p = 0.038) but also with day length (F = 11.455, p = 0.001), whereas it did not vary with breeding method (F = 1.525, p = 0.219), or sex (F = 0.006, p = 0.939). The distance travelled per h decreased with increasing age (Fig. 4), whereas the distance travelled per day did decrease with increasing age in winter (day length < 12 h), but not in summer (day length > 12 h).

Blueberries and cowberries constituted more than half of the food consumed by capercaillies throughout the year (Table 2). We observed birds consuming stones 34 times in 139 days (1 stone every 4 days on average), and on 13 occasions, they ate snow. Feeding on berries peaked during June and July, when fruits were readily available (Fig. 3B). During the summer months, capercaillies supplemented their diet by feeding on fresh grass and sedge, whereas in fall, winter and early spring they fed more on pine needles (Fig. 3B–C).

Discussion

Our study showed that released, captive-bred capercaillies can adjust to natural conditions. Duration of activity, daily movements and foraging behaviour of released capercaillies were similar to those of wild capercaillies observed elsewhere
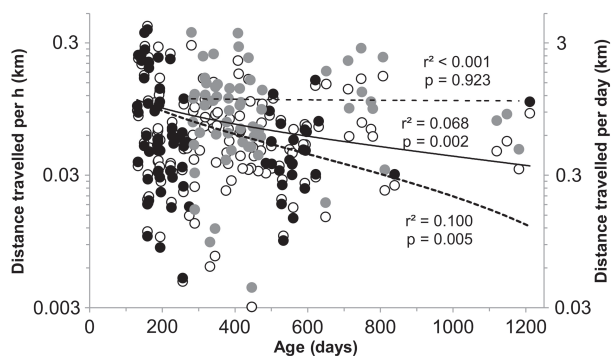

Figure 4. Logarithmic relation between age and distance travelled per h (open dots with continuous regression line) and distance travelled per day (black dots with dotted regression line for day length < 12 h; grey dots with dashed regression line for day length of > 12 h) of 22 young capercaillies radio-tracked for 139 full days.

(Gjerde and Wegge 1987, Picozzi et al. 1996, Summers et al. 2004, Gregersen and Gregersen 2008, Stader et al. 2013). The diet and foraging patterns indicate a sufficient availability of diverse natural food resources in the study area. Observed leks, broods (Merta et al. 2015) and successful reproduction confirmed by genotyping (R. Rutkowski, Museum and Inst. of Zoology, Polish Academy of Sciences, pers. comm.) furthermore point at the ability of released captive-bred capercaillies to cope with natural conditions. Considering data on mortality of the reintroduction programme in the Lower Silesia Forest (Merta et al. 2015), we conclude that reintroduction of captive-bred capercaillies can be successful if the initial mortality is reduced to an acceptable level.

In our study, capercaillies had one activity peak, only preening and feeding patterns were bimodal. However, capercaillies studied using radio-tracking in winter adjusted their daily activity patterns and time for roosting to sunrise and sunset (Gjerde and Wegge 1987). In their study, they estimated activity on the basis of changes in radio-transmitter signal strength, which resulted in bimodal activity patterns. However, activity estimated by changes in signal strength is not directly representative for time spent active (Rouys et al. 2001), but rather follows the same pattern as movements (Theuerkauf and Jędrzejewski 2002). We therefore believe that the bimodal activity patterns in the study of Gjerde and Wegge (1987) were caused by bimodality in movements.

Capercaillies were active approximately half of the daytime. Most of the active time was spent feeding. Feeding time was extended during the plant growing season, probably to maximise energy intake and increase body mass before winter. In winter, mean feeding time was unrelated to the length of day and remained at 3 h comparable to winter activity recorded in Norway (Gjerde and Wegge 1987).

Merta et al. (2015) showed that capercaillies reared and released in the presence of their mothers have smaller cumulative ranges over the first 75 days after release than birds reared and released without their mother. In this study, daily ranges of birds > 135 days old were not different when comparing the two groups. Therefore, the difference in exploration of the new environment between the two groups was not due to difference in daily mobility but rather by the lack of site fidelity (Giuggioli and Bartumeus 2012) in capercaillies released in the absence of their mother.

The diet of capercaillie in our study consisted of berries, shoots, leaves, needles and grasses and sedges and was similar to those in other sites of central and northern Europe (Picozzi et al. 1996, Summers et al. 2004). Although, unlike in boreal forest, where capercaillie feed almost exclusively on pine needles, shoots and cones in winter (Pulliainen 1979), the diet in our study was diverse year-round. In the Lower Silesia Forest snow cover is usually low (a few cm) and lasting for a maximum of 40 days, therefore cowberries and shoots of blueberry and cowberry are available throughout the winter. Supplementing winter diet with berries and shoots is energetically beneficial and may reduce winter mortality. We conclude that the behaviour of released young is similar to that of wild adult birds. Therefore we think that this study also provides data improving our knowledge on the general ecology of capercaillies.

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