

Article

First Record of the Red-Footed Falcon's Nocturnal Flight Activity during the Nestling Period Using GPS Data

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Abstract: The red-footed falcon (*Falco vespertinus*) is a species that is of great interest to conservation. Because of this, understanding the red-footed falcon's flight behavior is important for the conservation of this species. In this context, by using accurate GPS data-loggers, in 2019 and 2020, we analyzed its flight activity at the two largest colonies in Italy, and we collected 5840 GPS points. At night, all of the surveyed individuals were active during all of the hourly intervals, and they were in flight for about 10% of the time (40% in the daytime). The nocturnal flight activity showed a dual pattern: frequent and long-distance flights before sunrise (22.22% of time in flight; maximum distance from nest > 3 km) and after sundown (32.14% of time in flight; maximum distance from nest > 12 km), and limited and short-distance flights late at night (10 p.m.–5 a.m.; <5% of time in flight; maximum distance from nest < 100 m). Our study suggests that an increase in alfalfa crops and fallow land (in place of maize and soy crops) in the surroundings (i.e., 50–100 m) of the nests would considerably help this species to avoid, or at least to minimize, nocturnal flight activity, with expected improvements in its reproductive success. Our results are a step forward in advancing the knowledge of this important red-footed falcon population, which has been largely unknown so far. We provide here the first evidence ever of the red-footed falcon's regular nocturnal flight activity during the nestling period (June–July).

Keywords: biotelemetry; distance from nest; *Falco vespertinus*; flight behavior; flight height; flight speed; Italy; movement ecology; threatened species



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1. Introduction

The red-footed falcon (*Falco vespertinus*) is a raptor species that breeds in open rural environments that are predominated by extensive cultivation and pasture and the presence of rows of trees [1], and it is classified as a vulnerable species, both at the global and European levels [2,3]. Its recent decline is attributable to habitat degradation, pesticide spraying, and the conversion of grasslands to agricultural fields [2].

Recently, nocturnal flight activity has been documented for several raptor species that had been previously described as only diurnal [4–8]. By contrast, although the red-footed falcon has been widely studied [9–12], it is still considered a typically diurnal species, and nothing has been reported so far about its nocturnal activities. In this work, we investigated the red-footed falcon's flight activity at the two largest colonies in Italy, and we provide, for the first time, evidence of the regular nocturnal flight activity of this species during the nestling period (i.e., the interval between hatching and fledging).

By using accurate GPS data-loggers, we analyzed the red-footed falcons' population in the province of Parma (Italy) (Figure 1), which is an area that hosts more than 90% of the red-footed falcons' population breeding in Italy [13]. In 2020, we censused 82 breeding pairs in two colonies that are located within two Natura 2000 sites (SPA IT4020018 and SAC-SPA IT4020017). This rural environment presents isolated rows of black poplar (*Populus nigra*) and oak (*Quercus robur*) trees for nesting and roosting, and foraging areas that consist of alfalfa (*Medicago sativa*) crops. We aimed to: (a) Analyze the red-footed falcon's flight

activity at these two largest colonies in Italy during the nestling period; (b) To compare the night-time vs. daytime flight activities; (c) To compare the June vs. July flight activities; and (d) To advance explanations for the unexpected nocturnal flight activity. This study represents a contribution to the knowledge of this red-footed falcon population, which has been relatively unknown so far.

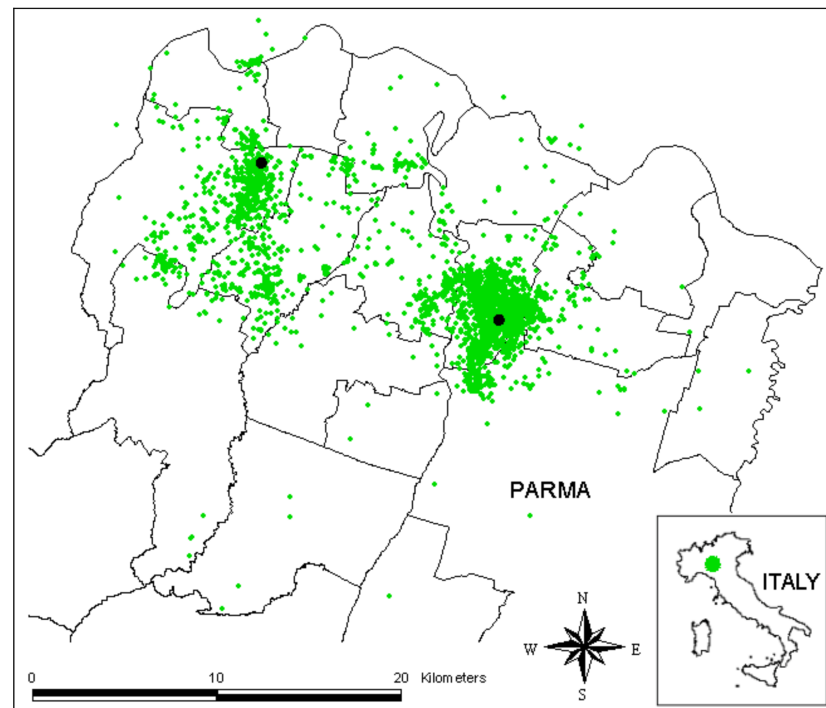


Figure 1. Study area (the province of Parma, Italy). Municipalities and 5840 GPS points (green dots) of the tracked red-footed falcons are shown. Black dots indicate the two red-footed falcon colonies (Colony A on the left, and Colony B on the right).

2. Materials and Methods

We tracked four adult (>2 years old) red-footed falcons during 16 June–22 July 2019 and 2020 (Table 1). The falcons were in fit health conditions and belonged to four different nests, in order to avoid pseudoreplication [14]. We used decoy birds (eagle-owls and Harris’s hawks) and mist nets to capture the birds near their nests. By using a 2 mm-large Teflon tape with a triple simple knot, we tied accurate TechnoSmart RadioTag-14 miniature data-loggers dorsally to the base of the central tail feathers, and, at the height of the sternum, two tapes were crossed without a knot and were fixed by seams so that the birds could fly freely. The RadioTag-14 loggers make use of a wireless system for data downloads when the base station antenna is within 400 m from the tracked individuals. The loggers collected information about the date, time, latitude, longitude, instantaneous flight height a.s.l., and flight speed (*FS*) (m/s). We only used GPS points with an HDOP (horizontal dilution of precision) ≤ 5 (i.e., ideal (HDOP = 1), excellent (HDOP = 2), or good ($3 \leq \text{HdoP} \leq 5$) positional measurements). The protocol and procedures that were employed were ethically reviewed and approved by the ISPRA (Italian Institute for Environmental Protection and Research) and were conformed to Directive 2010/63/EU. Each GPS point was labelled as “daytime” or “night-time” on the basis of the daily data on the sunrise and sunset in Parma, which is available at: <http://www.sunrise-and-sunset.com/en/sun/italy/parma> (accessed on 23 December 2021). Sunset took place at about 9:00 p.m. local time (9:06 p.m. on 16 June, and 8:56 p.m. on 22 July), and sunrise took place at about 5:45 a.m. local time (5:34 a.m. on 16 June, and 5:56 a.m. on 22 July).

Table 1. Description of the tracked red-footed falcons. Refer to Figure 1 for the positions of Colonies A and B within the study area.

GPS ID	Colony	Sex	Start of Tracking	End of Tracking	GPS Points
5001	A	M	16 June 2019	22 July 2019	1707
5002	A	F	16 June 2020	22 July 2020	1137
5003	B	M	16 June 2019	22 July 2019	721
5004	B	M	16 June 2019	22 July 2019	2275

Data acquisition occurred every 15 min so as to minimize the spatial autocorrelation [15]. Field surveys allowed us to locate the nests and roosts that were used by the tracked individuals.

GPS data were imported into GIS and superimposed onto: (a) The boundaries of the province of Parma; (b) Digital orthophotos at a 1:500 scale; (c) A terrain elevation a.s.l. at a 1:1000 scale; and (d) The nest and roost locations. For each GPS point, we calculated the distance from the individual's nest (DN) (in meters) and from the nearest roost site (DR) (m). The flight height above ground level (FH) (m) was calculated for each GPS point by subtracting the terrain elevation a.s.l. from the flight height a.s.l., which were provided by the data-loggers. By using digital orthophotos, we estimated the radius of the black poplar and oak tree canopies that were used for the nesting and roosting activities to be about 1 m. Therefore, the GPS points were classified as flight activity if $FS > 0$ m/s, $FH > 0$ m, $DN > 1$ m, and $DR > 1$ m (i.e., if the birds were moving in the air and were outside the rows of the black poplar (*Populus nigra*) and oak (*Quercus robur*) trees that were used for nesting and roosting). We used the upper-tail paired t -test [16] to compare the individuals' flight attributes on a daytime vs. night-time basis. p -values < 0.05 were regarded as statistically significant.

3. Results

The available dataset added up to 5840 GPS points (Figure 1). Overall (i.e., with data from all the individuals pooled), the tracked red-footed falcons were found in flight for 33.16% of the time (1936 GPS points out of 5840; Figure 2): 39.87% during the daytime (1806 points out of 4529), and 9.94% at night (130 points out of 1308).

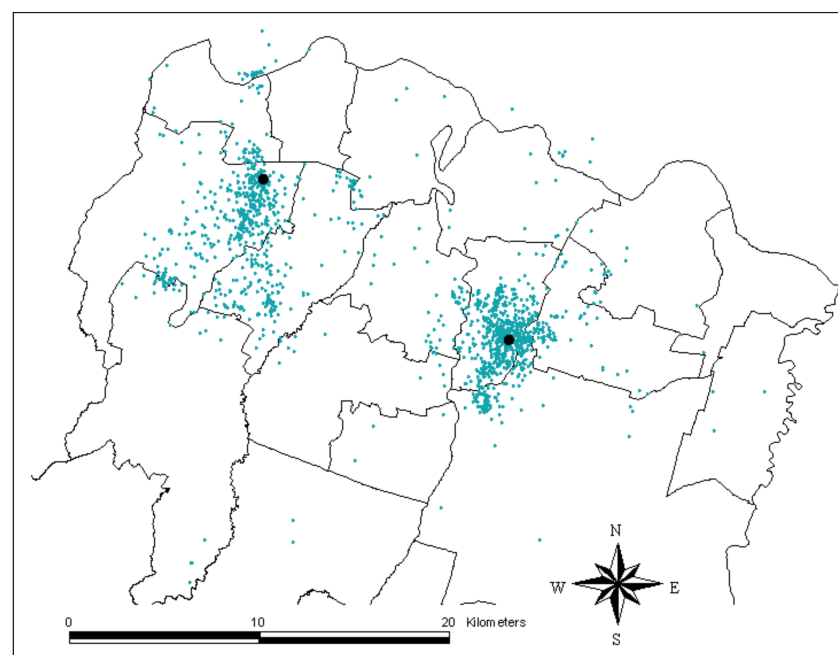


Figure 2. The subset of 1936 GPS points depicting the tracked red-footed falcons in flight.

On an hourly basis, the flight activity of the tracked birds was unevenly distributed (Figure 3), with two peaks between 10 and 11 a.m. (55.94% of time in flight; 160 GPS points out of 286) and 4 and 5 p.m. (47.89%; 182 GPS points out of 380). At night, all of the tracked red-footed falcons were active during all of the hourly intervals. The nocturnal flight activity showed a dual pattern (Figure 3): it was frequent in the two hourly intervals of 5–6 a.m. (22.22% of time in flight; $n = 18$ GPS points, of which 16 were in the 5–5.30 a.m. interval) and 9–10 p.m. (32.14% of time in flight; $n = 84$), and it was limited late at night (10 p.m.–5 a.m.; <5% of time in flight).

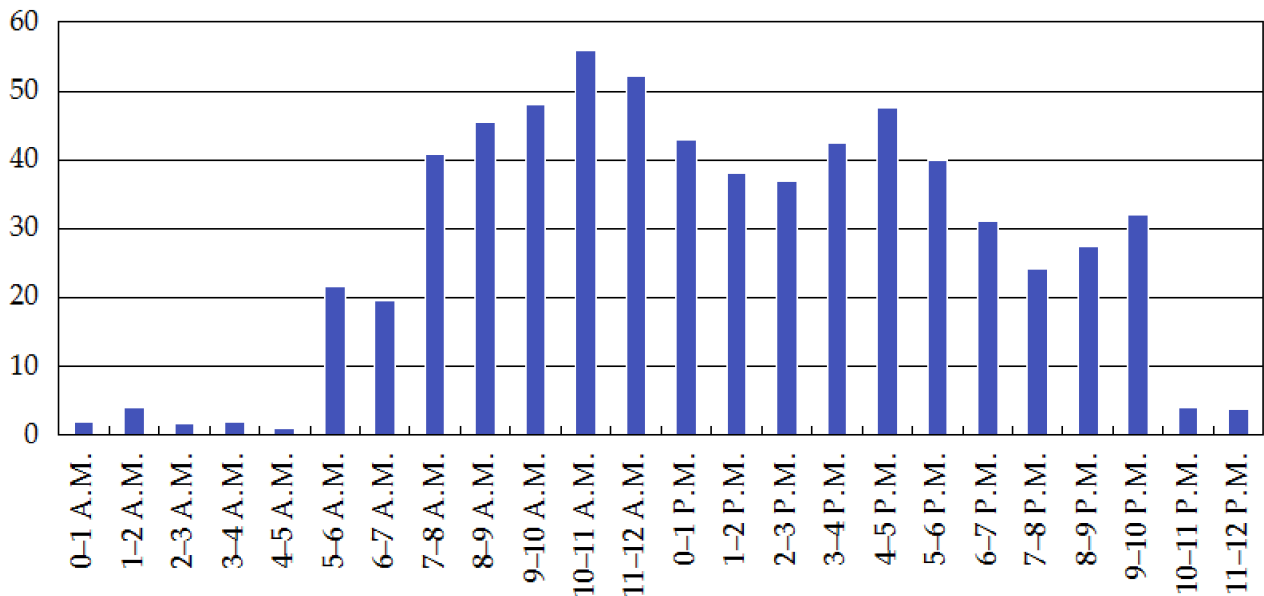


Figure 3. For each time interval (local time), the percentage of time that the tracked red-footed falcons were in flight is shown.

On average, the diurnal *FH* was 2.5 times higher than the nocturnal one (116.8 vs. 46.1 m, respectively; Table 2), while the diurnal *FS* and *DN* were 11.48% (6.8 vs. 6.1 m/s, respectively) and 14.65% (2418 m vs. 2109 m, respectively) higher. The maximum *DN* was almost twice in the daytime (21,470 m) than it was at night (12,083 m). Two flight attributes (*FH* and *FS*) were significantly higher in the daytime than at night. The female red-footed falcon (ID: 5002) showed very low values of the mean and maximum *DN* at night, and, by contrast, it exhibited the highest value of the maximum *DN* in the daytime (21,470 m).

Table 2. Flight attributes of the four red-footed falcons tracked. *FH*: flight height above ground level (meters); *FS*: flight speed (m/s); *DN*: distance from nest (meters). * $p < 0.05$, ** $p < 0.01$.

GPS ID	Mean <i>FH</i>		Mean <i>FS</i>		Mean <i>DN</i>		Maximum <i>DN</i>	
	Day	Night	Day	Night	Day	Night	Day	Night
5001	143.7	55.0	7.3	6.0	3307.4	3348.1	9654	7819
5002	90.8	47.3	6.1	2.6	2026.3	80.5	21,470	378
5003	118.2	41.2	5.9	4.2	1425.0	1939.6	9861	7320
5004	99.0	39.8	7.5	6.8	2128.0	1440.6	15,608	12,083
Upper-tail Paired <i>t</i> -test	$p = 0.0033$ (**)		$p = 0.0291$ (*)		$p = 0.2021$		$p = 0.1076$	
Overall	116.8	46.1	6.8	6.1	2418.7	2109.8	21,470	12,083

On a monthly basis (Table 3), the differences between day and night decreased considerably in July, when the mean *DN* was higher at night.

Table 3. Flight attributes by month using data from all individuals pooled.

Month	Mean FH		Mean FS		Mean DN		Maximum DN	
	Day	Night	Day	Night	Day	Night	Day	Night
June	127.7	37.1	6.4	5.2	3056.4	1668.8	21,470	12,083
July	111.7	50.5	7.1	6.6	2122.8	2354.7	10,080	7817
Overall	116.8	46.1	6.8	6.1	2418.7	2109.8	21,470	12,083

On an hourly basis, clear patterns emerged (Table 4).

Table 4. Time intervals (local time) and red-footed falcons' flight attributes using data from all individuals pooled.

Time Interval	Day/Night	Mean FH	Mean FS	Mean DN	Maximum DN
0–1 a.m.	N	25.67	0.49	30	66
1–2 a.m.	N	37.60	0.70	15	35
2–3 a.m.	N	56.50	1.30	56	56
3–4 a.m.	N	35.50	1.25	20	20
4–5 a.m.	N	64.00	0.48	29	29
5–6 a.m.	N/D	45.11	6.94	685	3116
6–7 a.m.	D	62.33	6.03	2626	7324
7–8 a.m.	D	62.87	7.43	3681	7736
8–9 a.m.	D	62.07	6.64	2690	10,309
9–10 a.m.	D	80.59	6.33	2399	14,399
10–11 a.m.	D	88.71	7.24	2246	11,966
11–12 a.m.	D	101.35	6.66	2079	11,559
0–1 p.m.	D	114.23	7.12	2137	14,113
1–2 p.m.	D	113.21	6.56	2010	13,759
2–3 p.m.	D	156.97	8.08	2938	20,871
3–4 p.m.	D	173.91	7.32	2911	21,470
4–5 p.m.	D	165.68	7.63	2342	11,474
5–6 p.m.	D	170.12	6.42	2082	12,345
6–7 p.m.	D	89.49	6.16	2407	11,259
7–8 p.m.	D	56.67	5.49	2859	11,486
8–9 p.m.	D	53.76	6.89	2686	11,446
9–10 p.m.	N	47.61	7.92	3278	12,083
10–11 p.m.	N	48.13	0.63	21	36
11–12 p.m.	N	35.14	0.86	15	25

On average, the FH was highest between 5–6 p.m. (170.12 m; $n = 159$ GPS points in terms of the birds' flight activity), while the FS was highest between 2–3 p.m. (8.08 m/s \cong 29.08 km/h; $n = 146$). The lowest values of the FH (25.67 m) and the FS (0.49 m/s \cong 1.76 km/h) were recorded at night, between midnight and 1 a.m. On average, the DN was the highest (3.68 km) between 7 and 8 a.m. At night, the mean DN was < 60 m for all the hourly intervals, except for before sunrise (5–6 a.m.; mean DN = 685 m; $n = 18$, of which 16 were in the 5–5.30 a.m. interval) and after the sunset (9–10 p.m.; mean DN = 3278 m; $n = 84$). In the daytime, the mean DN was at the minimum during the hottest time interval (1–2 p.m.; mean DN = 2010 m; $n = 151$). The maximum DN was highest in two consecutive intervals: 2–3 p.m. (maximum DN = 20,871 m; $n = 146$) and 3–4 p.m. (maximum DN = 21,470 m; $n = 158$). At night, the maximum DN was always < 70 m, except for the two intervals: 5–6 a.m. (maximum DN = 3116 m; $n = 18$, of which 16 were in the 5–5.30 a.m. interval) and 9–10 p.m. (maximum DN = 12,083 m; $n = 84$).

According to our results, at night: (i) The red-footed falcons were found in flight for about one-tenth of the monitoring time, with flights up to 12 km from the nest; (ii) All the surveyed red-footed falcons were active during all the hourly intervals, with respect to the daytime; (iii) They flew lower and slower; and (iv) They were closer to the nest in June, but not in July. The nocturnal flight activity showed a dual pattern: frequent and

long-distance activity before sunrise and after sundown, and limited and short-distance activity late at night.

4. Discussion

We found unexpected nocturnal flight activity by investigating the flight behavior of the largest red-footed falcon population in Italy.

With regard to the reasons behind this unexpected nocturnal flight activity, our results allowed us to discard several incorrect hypotheses. First, some individuals might be able to benefit from artificial light and may not be concerned about flying close to villages and roads, even at night [11]. Second, the tracked red-footed falcons could have realized detailed knowledge of the study area, and they could thus be confident in flying at night as well [11]. Third, as the average difference in the temperature between day and night was high during the tracking period (10.4 °C in June and 10.8 °C in July; data from the meteorological office of the Emilia-Romagna region), it could be energetically advantageous for the red-footed falcons to fly at night. However, these hypotheses are in clear contrast to the detected evidence that the red-footed falcons' flight activity was considerably more intense during the daytime, and they are also contradictory to the evidence that nocturnal flights were more frequent just before sunrise and after the sunset, which thus suggests that the sunlight, even when very low, was supportive of the red-footed falcons' flight activities. We can also exclude nocturnal disturbances by other bird species that could have provoked off-nest flights. A sensory tradeoff that led to a visual modification might have produced a stronger selection for nocturnal vision in some red-footed falcons, which has already been found in several raptor species [17]. Nonetheless, it seems highly improbable that this visual modification might have affected all of the individuals that we randomly chose in the two colonies under study. Adverse weather conditions may sometimes result in the sudden abandonment of the nest; however, it is implausible that this reason explains regular nocturnal flights, such as those recorded in this study.

Accordingly, we advance two explanations. First, the recorded nocturnal flights were partially due to flights from/to the roost sites. The individual 5001 (Colony A) started its nocturnal roosting activity at the largest roost site in the province of Parma (about 2.9 km northeast of its nest) on 10 July 2019, and occasionally continued until 22 July. The individuals 5002 (Colony A) and 5003 (Colony B) were never found close to the roost sites during the tracking period. At night, the individual 5004 (Colony B) made use of opportunistic (i.e., small and rarely used) roost sites that were 3 km north of its nest on 23 June and 18 July 2019, and also on 18 July and 19 July 2019, in a row of trees that were 800 m south of its nest. Flights from the nests toward the roost sites, and vice versa, primarily occurred in the hourly intervals after sundown and before sunrise, and, thus, they explain, in part, the frequent and long-distance flights in these two hourly intervals. The second explanation deals with foraging requirements. The red-footed falcon is a short-grass specialist that feeds upon different food resources (insecta, amphibia, reptilia, and mammalia), and whose hunting efficiency is more influenced by prey reachability than by prey abundance [9–12]. The loss and degradation of its foraging habitat is mostly due to the intensification of agriculture [18]. In recent years, both the substitution of optimal foraging patches in favor of maize and soy crops, as well as disadvantageous grassland management techniques (in particular, a decrease in the extent of fallow land), occurred around these two colonies. Because of the degradation of the foraging habitat, it is plausible that there was insufficient time during the daylight hours to find enough prey to feed both the offspring (in 2020, we counted 2.7 ± 0.76 std. dev. chicks per nest in Colony A, and 3.1 ± 0.92 std. dev. chicks per nest in Colony B) and parents. We therefore suggest that the nocturnal flights in the 10 p.m.–5 a.m. interval were mostly aimed at supporting short-distance hunting activities. In fact, the analysis of the hunting behavior of this population reveals that almost 40% of the hovering–perching activity occurred within 50 m from the nests, and that this occurred at night as well [19].

A comparison with the recently detected nocturnal flight activities of the lesser kestrel (*Falco naumanni*) [3,4] indicates that the red-footed falcons flew shorter distances at night. The reason arguably relies on the fact that the lesser kestrels in Southern Italy dwell in urban colonies and have foraging habitats that are several km distant from their nests [20]. By contrast, the red-footed falcons in the province of Parma live in a rural environment that, although it has been degraded and modified in the last few years, still offers few optimal foraging patches (alfalfa crops and fallow land) and extended arable fields with low prey abundance in the close surroundings of the nests. Instead, we found the same pattern with regard to the flight height above ground level and, in fact, this flight attribute was about 2.5 times higher in the daytime than at night, which is also the case with the lesser kestrels [21]. We argue that, at night, both species were forced to fly lower in order to maintain an adequate visual resolution to detect preys. In fact, birds' eyes are described by visual acuity (the ability to see fine details) and visual sensitivity (the skill to see at low-light levels), and there is a trade-off between them: when there is little visual information because of lower light levels, the visual resolution cannot be high [22]. It should be noted that, while the precision of the TechnoSmart RadioTag-14 miniature data-loggers in terms of the horizontal components (latitude, longitude, and flight speed) is very elevated (i.e., submetric when the HDOP ≤ 5 , as in this study), the error that is associated with the vertical component (flight height) could be up to a few meters; however, errors are normally distributed around the true values and, therefore, the mean *FH* values that are used in this study are well representative of the true ones.

5. Conclusions

Our study documents the red-footed falcon's flight behavior at the two largest colonies in Italy during the nestling period. In addition, it first discloses the regular nocturnal flight activities of a species that has previously been described as only diurnal, and it also provides an explanation for this unexpected activity.

Moreover, our study suggests that, at night, the red-footed falcons were forced to fly in the surroundings of their nests in order to support their hunting activities. The recent degradation of the foraging habitat has probably led to a situation where there was insufficient time in the daytime to find enough prey to feed both the offspring and the adults. We argue that this regular nocturnal flight activity is energetically expensive and that it also prevents these birds from carrying on their activities in the nest (e.g., presence at nest for resting, parental cares, social interactions, driving away intruders, etc.). From a conservation viewpoint, our study indicates that an increase in alfalfa crops and fallow land (in place of maize and soy crops) in the surroundings (i.e., 50–100 m) of the nests would help this species considerably to avoid, or at least to minimize, its nocturnal flight activity, with expected improvements in the reproductive success. As the two colonies that are considered here are located within two Natura 2000 sites, this conservation measure should be included in their management plans as soon as possible.

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Informed Consent Statement: Not applicable.

Data Availability Statement: The dataset used in this study is available from the first author upon reasonable request.

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