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RESEARCH ARTICLE

Phenology, variation in habitat use, and daily activity patterns of Eleonora's falcon overwintering in Madagascar

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Abstract
Context The vast majority of the global population of Eleonora's falcon overwinters in Madagascar, where the natural environment is threatened by human-induced habitat changes, particularly intensive forest degradation.
Objectives We described Eleonora's falcon phenology and habitat use based on fine-scale telemetry data and field surveys, and investigated which environmental parameters shape the observed patterns, to obtain a better insight into the species' ecological requirements during the wintering season.
Methods We used high resolution GPS telemetry and remotely sensed data to establish bird–habitat associations and investigate spatiotemporal activity. We also verified habitat composition through ground surveys.
Results Eleonora's falcon exploits a variety of habitats, exhibiting a distinct phenological pattern in their use. The species exhibits high site fidelity, moving progressively from more open areas towards landscapes with denser tree cover, possibly as a response to spatiotemporal patterns in food abundance. Time budget analysis revealed that Eleonora's falcon dedicates just about 15% of its daily activity to foraging, which is performed almost exclusively during daylight hours, with a greater tendency to forage at higher elevations with denser tree cover. On-site assessment of habitat composition revealed that existing habitat maps overlook small fragments of habitat and land use. However, the species' overall preference for humid forest suggests ongoing deforestation would adversely affect the availability of preferred habitat.
Conclusions Our findings suggest that GPS logger technology, when combined with ground surveys, can enhance our understanding of long-distance migratory bird species' ecology at finer and more ecologically relevant scales.

Keywords *Falco eleonorae* · Telemetry · Ground-truthing · Fidelity · Humid forest · NDVI

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Introduction

Long-distance migratory birds are potentially exposed to multiple threats by occurring in geographically distinct areas during their annual cycle (Newton 2004; Sanderson et al. 2006) and thus are subject to carry-over effects. For example, wintering habitat deterioration can incur downstream effects at subsequent life-cycle stages, including breeding success, especially for insect feeders overwintering in Africa (Norris et al. 2004; Brown and Sherry 2006). Yet, knowledge of the ecology of Afro-Palearctic migrant species at their wintering grounds is far less comprehensive than at the breeding grounds (Sherry and Holmes 1996; Sanderson et al. 2006). Advances in the production of miniaturized GPS tracking devices have allowed tracking of smaller birds for short-term studies e.g. at the breeding grounds (Guilford et al. 2008; Kotzerka et al. 2010) or during migration (Guilford et al. 2011). But to date long-term studies encompassing the wintering period for small and medium-sized birds have thus far been restricted to the use of less accurate devices, such as satellite transmitters (Meyburg et al. 2011; Limiñana et al. 2012) and geolocators (Catry et al. 2011; Jacobsen et al. 2017; Xenophontos et al. 2017).

Eleonora's falcon (*Falco eleonorae* Géné, 1839) is a medium-sized, obligate, trans-equatorial migrant species (Pulido 2007; Kerlinger 2008). It breeds primarily in the Mediterranean region, while it over-winters (i.e. spends the austral summer months) in Madagascar (Walter 1979), and thus can be considered a 'double' endemic (Bildstein 2006). It is also regarded as one of the most ecologically finely-tuned falcons (Cramp et al. 1980). The species' delayed breeding season coincides with the passage of migratory birds over the Mediterranean Sea upon which it feeds during the rearing period of its offspring, while its post-breeding period in Madagascar ensures an abundance of insects, which comprise its primary food source for most of the year (Del Hoyo et al. 1994). However, intensive forest degradation in Madagascar (Harper et al. 2007; Grinand et al. 2013; Global Forest Change 2019) as well as historic climate change, might have already limited favourable habitats of Eleonora's falcon (Walter 1979). Thus, research needs to focus on the post-breeding period to gain a deeper insight into the species' ecological requirements (Ristow 1999; Barov and Derhé 2011).

Based on recent telemetry studies (compiled by Kassara et al. 2017), it was confirmed that populations throughout the breeding range overwinter almost exclusively in Madagascar. Habitat associations however have been investigated only at a coarse resolution of 1 km^2 (Gschweng et al. 2012; Mellone et al. 2012; Kassara et al. 2014), while detailed information on spatiotemporal activity patterns and daily budgets has been completely lacking thus far. For example, at the breeding grounds in the eastern Mediterranean the feeding window of Eleonora's falcon was found to cluster within a few hours per day (typically early morning and late afternoon) (Walter 1979). However, it is not known whether its foraging activity exhibits a similar pattern on wintering grounds, as found in other wintering raptors (Plumpton and Andersen 1997). Previous studies also suggest that vegetative cover affects Eleonora's falcon distribution (Gschweng et al. 2012; Mellone et al. 2012; Kassara et al. 2014), but little is known on the role of vegetative cover on non-breeding foraging activity. In addition, it has been shown that there is site fidelity at the individual level (Mellone et al. 2012; Kassara et al. 2017). Still, considering that habitat usage in raptors has been described as temporally variable following temporal patterns of food availability (Tapia et al. 2007), establishing home ranges on a progressive basis is necessary to identify possible within season progressive site fidelity. Furthermore, previous studies have provided some insight into the species' ecological requirements, showing that individuals tend to occur in heterogeneous habitats with small isolated patches of suitable vegetation (Kassara et al. 2014), and also forage at night (Buij and Gschweng 2017). Finer-scale research though is needed for a better insight into species–habitat relationships and daily activity patterns.

In spite of the finer tracking resolution that can be achieved using GPS technology, the lack of detailed information on landscape structure could be a critical limitation in such studies. Due to the fact that many habitat variables, such as stand structure and availability of single trees for perching require high-resolution remote sensing, which is not always available (Tapia et al. 2007), ground-truthing remains an essential tool in ecological studies (Mack et al. 1997; Garshelis 2000; Tapia et al. 2007). Furthermore, boundary delineation is prone to errors, while small patches of suitable habitats are likely to be misclassified in remote sensing studies (Rappole et al. 2003; Gottschalk et al. 2005). By contrast, ground-based mapping has better potential in unraveling species–habitat associations, especially in the case of highly fragmented habitats (Kremen et al. 1999). Thus, ground-based habitat mapping in combination with telemetry locations of high accuracy, such as the ones provided by GPS technology, is considered the most effective method to investigate species–habitat relationships (Gottschalk et al. 2005).

In this study we aimed to investigate the phenology of Eleonora's falcon during its wintering period in Madagascar, making use of GPS technology, remote sensing, and ground surveys to describe temporal fine-scale habitat relationships and daily activity patterns. Specifically, we used individually attached tracking devices to explore the daily and hourly patterns of activity of specific individuals originating from the eastern Mediterranean during the wintering (austral summer) period in Madagascar. We hypothesized that Eleonora's falcon in Madagascar would feed early in the morning and late in the afternoon as it does on its breeding grounds (Walter 1979), and that it would do so in relatively insect-rich areas (Kassara et al. 2017). We also investigated the spatiotemporal activity patterns and habitat usage on a monthly basis, to determine which habitat characteristics might influence observed progressive bird movements in Madagascar. We hypothesized that these movements might relate to the availability of food associated with increased rainfall. We also estimated home range sizes and spatiotemporal fidelity at a finer scale than previously possible, expanding on previous work (Kassara et al. 2017).

Moreover, we assessed for the first time the accuracy of currently available digital habitat maps at sites used by Eleonora's falcons in Madagascar. Because of ongoing deforestation in Madagascar (Global Forest Change 2019), habitat mapping could become rapidly outdated. So in addition to investigating habitat preferences using remotely sensed data, we performed on-site habitat mapping in Madagascar to verify habitat types in areas of species activity identified from tracking devices and compared our findings with existing habitat maps.

Materials and methods

Field methods

Between 2009 and 2017 we equipped 22 Eleonora's falcons originating from Greece and Cyprus with transmitters combining PTT (5 g and 9.5 g PTT transmitters, Microwave Telemetry) and GPS (GPS–GSM–UHF loggers, Ecotone Telemetry) technology. Specifically, 12 falcons were captured in Cyprus during the 2013 and 2014 breeding seasons, another four on an island in the central Aegean Sea in 2009 (see Kassara et al. 2012), and 6 more on an island in the Southern Aegean Sea during the 2015 and 2016 breeding seasons. Transmitters were attached with a Teflon harness as a backpack (Kenward 2000). The weight of the transmitters ranged between 1.5 and 5% of the birds' mass. No abnormal behaviour was observed after transmitter attachment (Barron et al. 2010), with individuals moving as expected between breeding and foraging areas over subsequent days. The PTTs attached to falcons in Cyprus were programmed to collect data (hereafter, PTT data) on a '10 h ON/48 h OFF' duty cycle, while the ones attached to falcons in the Aegean Sea were scheduled on a varying duty cycle for logistical reasons (see Kassara et al. 2012). All GPS loggers collected data every 5 h on average (range 1–6 h; hereafter, GSM data) and transmitted them via the GSM network. In addition the GPS loggers were also programmed to collect GPS data every 15–30 min; these GPS fixes (hereafter, UHF data) were stored in the loggers' memory and were retrieved for two falcons (one from Cyprus, and one from the Aegean Sea) via a base station antenna placed close to the falcons' nesting sites. Out of the 22 telemetry devices attached in total, 12 of them (6 GPS–GSM–UHF loggers and 6 PTT transmitters) provided data over the wintering period (Table 1).

Data filtering

The original dataset consisted of 25,752 locations (Table 1), including GSM, UHF and PTT data. We filtered out locations received during the first and last 7 days of each wintering event to account for migratory restlessness (Kassara et al. 2017). After calculating path metrics, i.e. distance and time interval between consecutive points and subsequently travel speed, we also excluded those positions indicating

Table 1 Details of the telemetry tracked individuals, the corresponding monitored wintering events and the number of retrieved locations from 2009 to 2018

S/n	Tag ID	Capturing location	Wintering event (s)	GSM	UHF	PTT	Unfiltered locations
1	CYPR01	Akrotiri (Cyprus)	2	236			236
2	CYPR03		4	2048	5002		7050
3	113739		1			422	422
4	113745		1			468	468
5	ELEF01	South Aegean (Greece)	1	661			661
6	ELEF02		2	1361	11,776		13,137
7	ELEF04		1	693			693
8	ELEF05		2	1147			1147
9	94118	Central Aegean (Greece)	1			440	440
10	94119		1			502	502
11	94120		1			379	379
12	94121		1			617	617
Total			18	6146	16,778	2828	25,752

unrealistic speed, i.e. over 80 km/h (Kassara et al. 2017). Because of the varying accuracy of PTT data (CLS 2013), we retained only high-quality locations, i.e. those corresponding to location classes LC3, LC2 and LC1 (Thorup et al. 2003). The filtered dataset (hereafter, datapool) consisted of 22,149 positions in total.

We used PTT and GPS data to delineate the individual home ranges, as well as to explore habitat use during each wintering event. To this end, from the datapool we retained locations at least 1 h and 1 km apart to minimize spatiotemporal autocorrelation (Otis and White 1999; Kassara et al. 2017). For the habitat use analysis we also excluded PTT data, whose spatial and temporal resolution prevented fine-scale assessment of bird–habitat associations. Furthermore, we explored the daily activity pattern of the two falcons for which UHF data were available, filtering out duplicate records, as well as consecutive locations more than 1 h apart to facilitate activity designation based on flying speed.

Daily activity

We explored foraging patterns of two falcons [ELEF02: winter 2016 (2016/2017) and 2017 (2017/2018); CYPR03: winter 2014 (2014/2015)], in relation to habitat features, including day and night differences, using nautical dawn and dusk to assign the obtained telemetry locations to day and night, thus accounting for the crepuscular ecology of the species (Walter 1979). We classified each path segment into four activity types judging by their corresponding speed, namely commute (> 20 km/h), forage (1–20 km/h), rest (< 1 km/h during the day) and roost (< 1 km/h during the night). Specifically, we examined the likelihood of foraging versus resting or roosting, with the use of binomial generalized linear mixed models (GLMMs). Explanatory variables comprised the date (with 1st November of each year assigned as day 1), and the following environmental variables: elevation (USGS 2016 at a 150 × 150 m nominal resolution); percent tree cover, using the vegetation continuous field product (VCF) from the moderate resolution imaging spectroradiometer (MODIS) sensor at a 250 × 250 m resolution (NASA 2018); and vegetation phenology, using the 16-day normalized difference vegetation index (NDVI) product again from the MODIS sensor at a 250 × 250 m resolution (NASA 2018). We also included in the GLMM all possible interactions of day and night with all continuous variables. Statistical analyses were performed in R 3.5.1 (R Core Team 2018) and spatial analyses in ArcGIS 10.1 (ESRI 2012), while sunlight was computed in R using the 'suncalc' package (Agafonkin and Thieurmel 2018).

Temporal patterns in habitat use

Visual inspection of the falcons' movements suggested that the birds moved to different areas more or less on a monthly basis. Thus, in order to elucidate whether these spatiotemporal patterns reflected changes in habitat preferences during the wintering period, we assessed habitat usage variability on a monthly basis using the most fine-scale data available to date, based on GSM data from six individuals. For one individual during one season (CYPR03-2014), a gap in GSM data was filled by UHF data covering the specific period, resampled to a 5-h interval based on the average sampling rate of all individuals. We examined whether: (a) areas visited by the falcons differed in elevation, VCF and NDVI; and (b) the frequency of habitat types used, as defined by the Madagascar vegetation mapping project (Moat and Smith 2007; resolution 250 $\times$ 250 m), changed during the wintering period. To this end, we separated the birds' locations into six monthly time-windows encompassing two 16-day NDVI granules each (16/10–16/11, 17/11–18/12, 19/12–16/1, 17/1–17/2, 18/2–21/3 and 22/3–22/4), and then extracted values for the aforementioned environmental variables. The first window had very few data points compared to the other windows therefore we excluded it from subsequent analyses. Specifically, we developed GLMMs using the lmerTest package (Kuznetsova et al. 2017) in R 3.5.1 (R Core Team 2018), to explore the effect of monthly window and breeding origin (fixed factors) and their interactions, as well as individual and year (crossed random factors), on the values of elevation, VCF and NDVI, controlling for the other two on each run. An interaction term was also considered between the breeding origin (hereafter, origin) and the monthly windows to account for possible differences in habitat preferences among individuals originating from different areas.

In order to investigate whether individuals change locations as a result of changing vegetation phenology we developed an additional GLMM model (hereafter NDVI temporal model) to contrast current NDVI values of the locations of a given time-window with the ones during the preceding and successive time-windows at the same locations. To further elaborate on progressive change in habitat type preferences, we developed GLMMs with a binomial distribution and logit link function in lmerTest in R. In particular, we developed six models, one for each of the most frequently used habitat types (i.e. cultivation, western dry forest, plateau grassland–wooded grassland mosaic, wooded grassland–bushland mosaic, humid forest and degraded humid forest). We assigned the value of one to the target habitat type and the value of zero to all the other habitat types. As above we included monthly window and origin as fixed factors, including their interactions, and individual and year as crossed random factors. For the final structure of all GLMMs, we used likelihood ratio tests, sequentially excluding non-significant variables (p value > 0.05) to identify potential model improvement as assessed via their AIC value (Zuur et al. 2009).

Home range and site fidelity

For each wintering event we delineated home ranges for every individual using utilization distribution (UD) estimates, based on 95% probability fixed kernels (Worton 1989), and then assessed inter- and intra-individual overlap based on the UD overlap index (UDOI; Fieberg and Kochanny 2005). In addition, we delineated the monthly (32-day windows) home ranges for those individuals with data from consecutive years and calculated monthly (same monthly period in consecutive years) site fidelity. Analyses were carried out in geospatial modelling environment (GME) 0.7.2.1 (Beyer 2012), ArcGIS 10.1 (ESRI 2012) and R 3.5.1 (R Core Team 2018) using the 'adehabitatHR' package (Calenge 2006).

On-site habitat mapping

We identified clusters of locations up to areas of 5 km^2, corresponding to more intensively used areas (Tapia et al. 2007), based on GSM and PTT (only LC3) data that were available by spring 2015. From a total of 27 clusters, we excluded 9 that we deemed inaccessible for our field work, resulting in 18 candidate clusters for on-site habitat mapping and assessment. In April 2015, due to logistical limitations and the inaccessibility of several sites because of flooding, we performed ground surveys at ten sites.

We used high-resolution satellite imagery (Google, Inc. 2013) for preparatory draft outlining of the habitat types through a desktop exercise (Grinand et al. 2013). Our goal was to assess the reliability of the Madagascar vegetation mapping project (Moat and Smith

2007) on a finer spatial scale. We thus retained the same classification scheme to facilitate comparison and analysis, but added subcategories where necessary to enable a more thorough qualitative assessment (Bibby et al. 2000), including habitat features matching the ecology of the species and reflecting its preferences (Bibby et al. 2000; Ausden 2004). During ground surveys we delineated the existing habitat types over the draft outline, aided by GPS readings where necessary (Bibby et al. 2000; Sutherland et al. 2004). We subsequently digitized the hand-drawn maps in ArcGIS 10.1 (ESRI 2012) and overlaid and compared the habitat type of bird locations on both the Madagascar vegetation mapping project layer and the on-site mapping layer. We examined the significance of differences between them with the use of χ^2 test.

Results

Daily activity

The two individuals that provided UHF data dedicated about 80% of their time either to resting or roosting and approximately 15% to foraging (Online Resource 1, Fig. S1), which was performed at different periods of the day. Specifically, ELEF02 tended to forage at any hour between 09:00 and 16:00 (local hour), while CYPR03 exhibited a bimodal foraging pattern, which peaked during the morning and afternoon hours (Fig. 1). The falcons were more likely to forage during daytime compared to night-time (89.1 and 10.9% respectively), and also in areas with higher elevation, higher VCF and lower NDVI; though foraging differences attributed to VCF and NDVI were less prominent during the night-time (Table 2). Foraging activity also appeared to decrease, though not significantly (P = 0.09), as the wintering season progressed.

Temporal patterns in habitat use

There was a progressive change in habitat use over the course of the wintering season (Fig. 2a–c; Online Resource 1: Table S1a–c). First, all tracked falcons, irrespective of their origin, moved to areas with increasingly greater tree cover (VCF) up to window 4 and from then on to areas with less tree cover (Fig. 2a). Second, while falcons from Greece occurred in more mountainous areas compared to those from Cyprus throughout the wintering season, the latter occurred progressively in higher elevations, whereas those from Greece visited lower elevations in the middle of the wintering season (windows 3 and 4), compared to the beginning and end of the season (Fig. 2b) Third, all individuals moved to areas of increased NDVI during the wintering season irrespective of origin (Fig. 2c). However, this pattern is likely an artifact since NDVI is expected to increase over time throughout the rainy season. Indeed, the NDVI temporal model indicated that if the individuals did not move to a new area on a monthly basis or arrived 1 month earlier at any given area, they would have encountered the same NDVI values (Fig. 3; Online Resource 1: Table S1d).

Moreover, the tracked individuals exhibited different habitat type preferences during the wintering

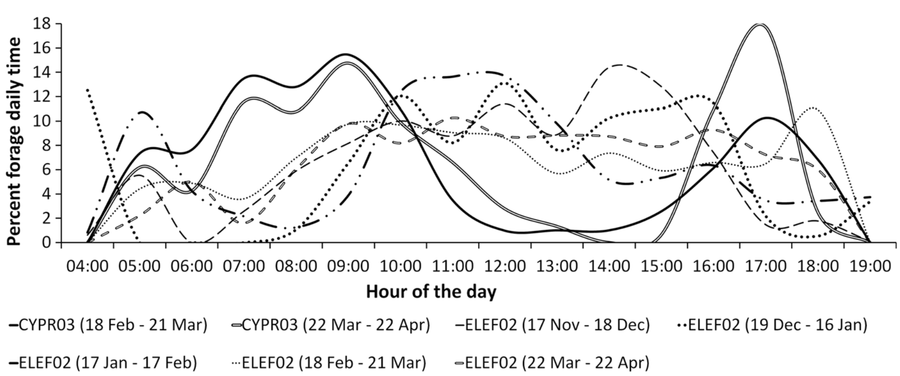


Fig. 1 Hourly distribution of foraging activity during daytime (expressed as percentage), grouped in 32-day (monthly) time-windows, for two individuals (three wintering events) that provided UHF data. A different foraging pattern (bimodal) was observed for CYPR03 (continuous lines) compared to ELEF02 (dotted/dashed lines), which tended to forage longer hours during the day

Table 2 Binomial GLMM results of the foraging likelihood based on locations (n = 13,842) obtained from the two individuals that provided UHF data

Variable	Estimate	SE	z	P
Intercept	− 1.12	0.26	− 4.29	< 0.001
Night	− 2.06	0.07	− 28.00	< 0.001
NDVI	− 0.09	0.03	− 2.93	< 0.01
VCF	0.37	0.04	10.06	< 0.001
Elevation	0.54	0.03	18.37	< 0.001
Date	− 0.05	0.03	− 1.67	0.09
Night: NDVI	0.12	0.08	1.41	0.16
Night: VCF	− 0.27	0.08	− 3.40	< 0.001
Night: elevation	− 0.41	0.09	− 4.61	< 0.001
Night: date	0.27	0.09	3.12	< 0.01

Foraging likelihood increases during daytime, and in areas with higher VCF (but less so during the night), lower NDVI and at greater elevation (but less so during the night). It decreases marginally though as the wintering season progresses

season (Fig. 2d), moving from more open areas (e.g. cultivations and grasslands) occupied during the first half of their stay in Madagascar, towards primarily the humid forest (intact or degraded) during the second half of the wintering period. They occupied different habitats as follows: (a) cultivations—the probability for falcons to occur in cultivations increased up to the middle of the wintering season and then decreased; (b) western dry forest—no linear pattern was observed; (c) plateau grassland–wooded grassland mosaic—no linear pattern was observed; (d) wooded grassland–bushland—an increasing occurrence probability was observed throughout the wintering season; (e) humid forest—individuals were most likely to be observed in humid forests up to window 5 and then less so; and (f) degraded humid forest—an increasing occurrence probability was identified throughout the wintering season (for full model results see Online Resource 1: Table S2).

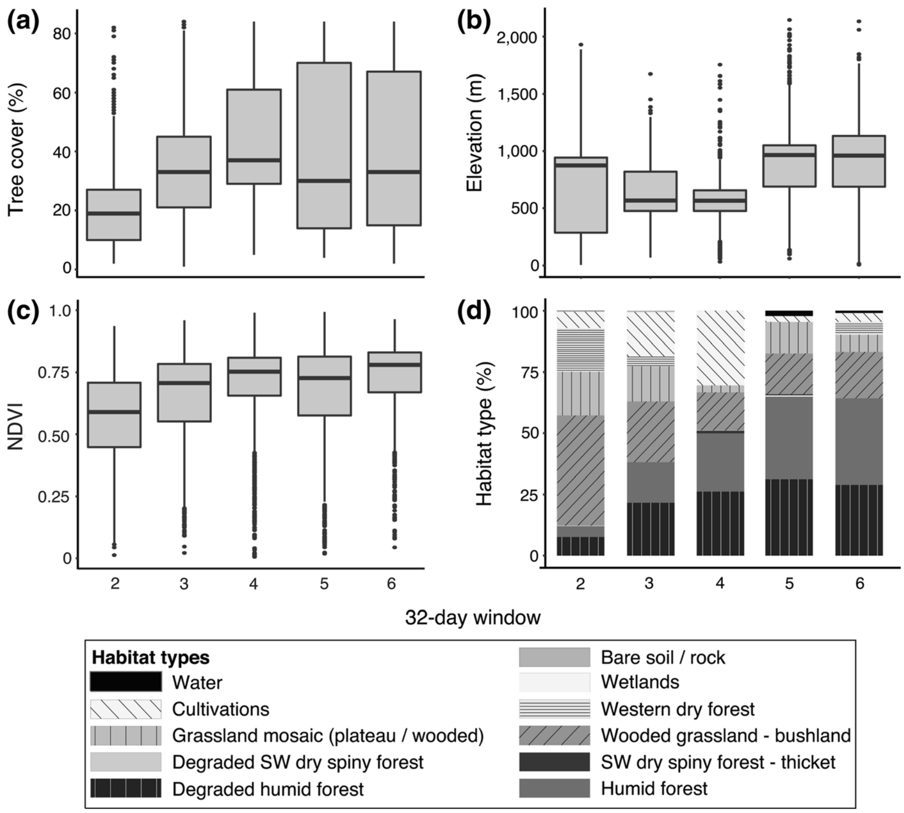


Fig. 2 Progressive change over the course of the wintering season (in 32-day windows) in: **a** percent tree cover-VCF, **b** elevation, **c** NDVI and **d** percent habitat type used (from Madagascar vegetation mapping project—see legend below figure for habitat types)

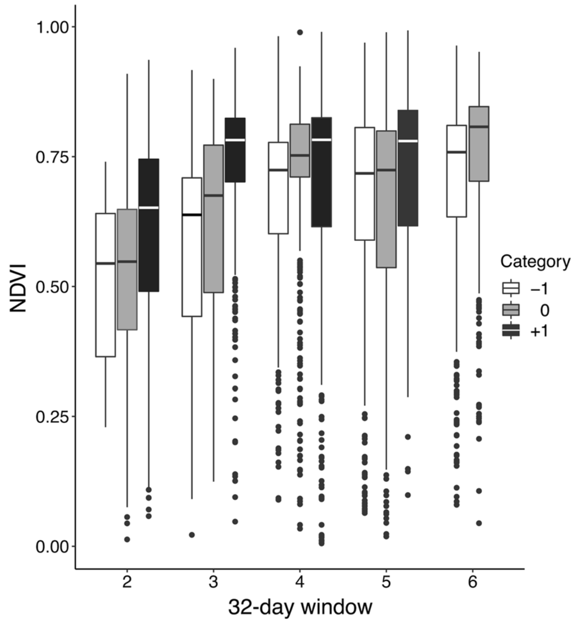


Fig. 3 Comparison of the NDVI values of the locations of a given time-window (grey columns; denoted with 0 in the legend), with the ones at the same locations during the preceding (white columns; denoted with − 1 in the legend) and successive (black columns; denoted with + 1 in the legend) time-windows

Home range and site fidelity

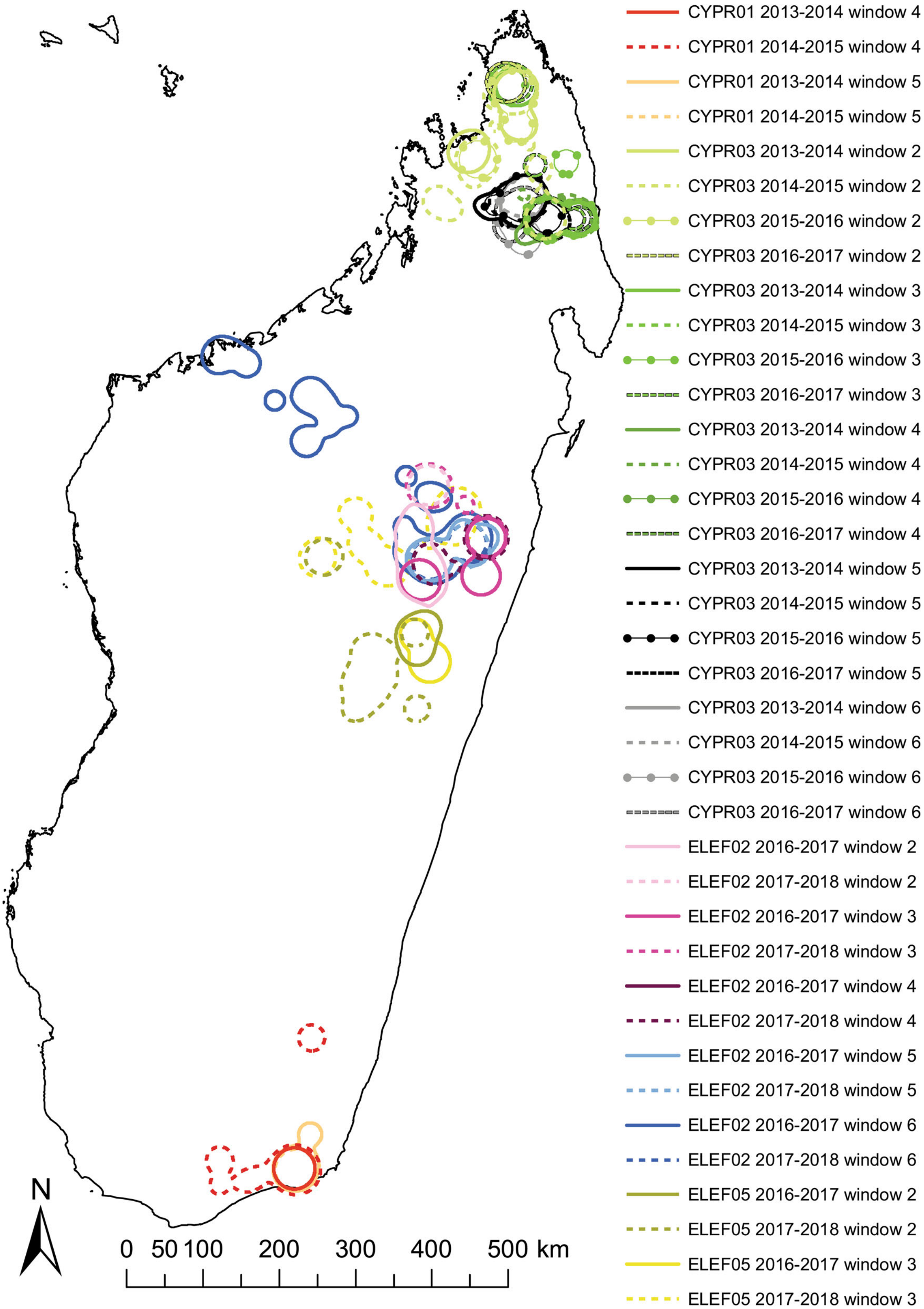
All tracked individuals in this study spent their winter exclusively in Madagascar, primarily roaming along the eastern part of the island (Online Resource 1: Fig. S2). Mean inter-individual overlap was estimated at 0.04 (SD = 0.08, N = 12), but there was evidence of intra-individual site fidelity. Falcons tagged in Cyprus had an intra-individual overlap estimated at 0.80 (SD = 0.49, N = 4) for CYPR03 and 1.03 (2 years) for CYPR01, while falcons tagged in Greece 0.65 (2 years) and 0.02 (2 years) for ELEF02 and ELEF05, respectively. This site fidelity was evident also on a monthly basis, with 61.43% of the area used in a specific monthly period (95% kernels), reused again during the same period in the following year (SD = 31.32, N = 24, Fig. 4).

On-site habitat mapping

On-site habitat mapping revealed some discrepancies between habitat types occupied based on the Madagascar vegetation mapping project (Moat and Smith 2007) and actual habitats identified during ground surveys [χ^2 (12) = 145.33, P < 0.001]. Although at a broad scale, the Madagascar vegetation mapping project reflects the habitats present on the ground, at a finer scale it was revealed that the falcons may occupy more open areas than what was indicated through the Madagascar vegetation mapping project (Online Resource 1: Table S3). In particular, several locations were found in wooded areas with extensive openings (wooded grassland–bushland mosaic), rather than in closed canopy forest (western dry forest) and in grassland with scattered trees (plateau grassland–wooded grassland mosaic) rather than wooded grassland (wooded grassland–bushland mosaic). In addition, small patches of certain habitat types and land uses, such as riverine forests, plantation forests and cultivations (e.g. rice fields and eucalypt plantations) were not distinguished on the Madagascar vegetation mapping project (Fig. 5).

Discussion

This is the first study to investigate daily activity patterns and estimates of daily time budgets during the day and at night in Eleonora's falcon wintering in Madagascar. This was made possible by utilizing the high temporal resolution in UHF data collection, combined with the high positional accuracy of GPS transmitters, which was not possible in previous studies using PTT data, for which data for day and night had to be pooled (Mellone et al. 2012). Despite the capacity of the species to fly up to 13 h per day (Rosén et al. 1999), we found that most of its time budget was devoted to rest during the day and roost at night, involving 19–20 h of the 24 h time budget, similarly to Ferruginous hawks (*Buteo regalis*) at their wintering grounds (Plumpton and Andersen 1997). Foraging was accomplished in 3.5 h on average per 24 h, almost exclusively distributed during daytime (between nautical dawn and dusk), which contrasts with previous findings for the species (Buij and Gschweng 2017). We suggest that previous reports of extensive night-time activity by Eleonora's falcon in Madagascar (Buij and Gschweng 2017) might reflect the temporal limitations of PTT transmitters. Foraging activity occurred in more forested areas and at higher elevations, where rainfall is higher, likely resulting in a higher abundance of insect prey, compared to the more open areas where the birds rest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ELEF02 2017-2018 window 6
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ELEF05 2017-2018 window 2
ELEF05 2016-2017 window 3
ELEF05 2017-2018 window 3
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0 50 100 200 300 400 500 km

◀**Fig. 4** Monthly (32-day windows) home ranges (95% kernels) of Eleonora's falcons from Greece (ELEF02 and ELEF05) and Cyprus (CYPR01 and CYPR03), which provided data for more than 1 year, illustrated on an outline map of Madagascar

and roost. The trend of a progressive decrease in foraging activity might suggest that individuals require less time to forage once they move to areas dominated by humid forest at higher elevations. There they may be able to quickly satisfy their dietary needs with less effort (Brandt and Cresswell 2009) foraging close to and within the humid forest where the abundance of insects is expected to increase as the rainy season progresses (Wolda 1978).

The distribution of Eleonora's falcon during the wintering period seems to follow a serial residency pattern (sensu Cresswell 2014), with transitions between geographically distinct areas at a monthly timescale, a pattern that is probably related to spatiotemporal patterns in food availability (Catry et al. 2011). Earlier field-based studies investigating the wintering range of Eleonora's falcon (e.g. Zefania 2001) suggested that any habitat type was equally suitable, including natural and human altered habitat types. Telemetry studies though provide unbiased localisation data unaffected by accessibility in the field (see Kassara et al. 2017) and reveal a preference for intact and degraded humid forest in areas with high elevation and rainfall. Here, using GPS telemetry and ground surveys, we found that upon arrival in Madagascar, Eleonora's falcon occurs first primarily in more open, drier habitats, such as wooded grasslands and bushlands, as well as western dry forests. They then move to more cultivated areas at lower elevations, which they gradually abandon in order to

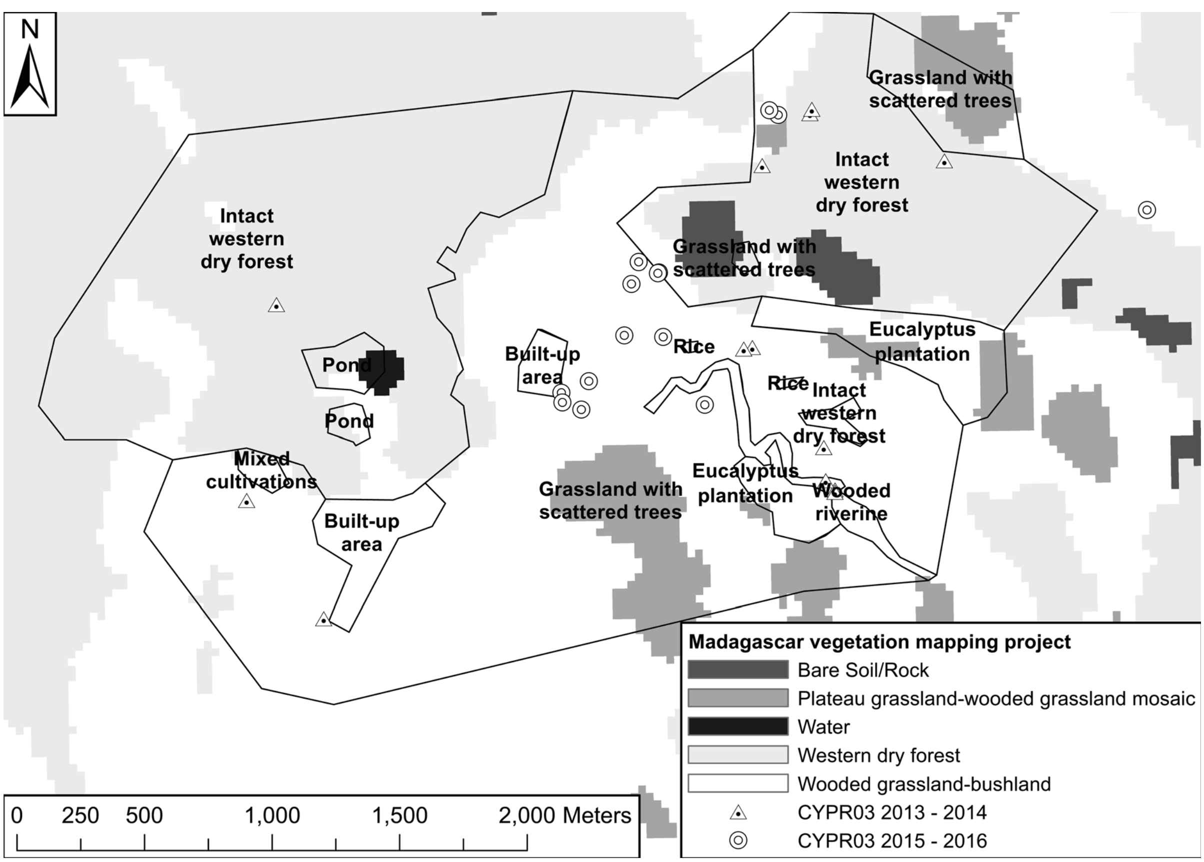

Fig. 5 Habitat type example comparison between Madagascar vegetation mapping project (grayscale raster with legend) and ground-truthing habitat mapping (black polygon outlines with habitat type names within them), for an area surveyed in 2015 at Ankarana National Park, northern Madagascar. General boundaries for larger polygons match condition on the ground, but important habitat/land use patches are not captured through Madagascar vegetation mapping project

converge on humid forest at higher elevations, where they spend most of the last 2 months of their time in Madagascar.

Movements to humid forest coincide with the rainy season between December and February (Moat and Smith 2007; Ghimire et al. 2017), taking advantage of the greater seasonal insect activity there then (Wolda 1988). Previous work suggested that individuals track changes in NDVI and seek more productive habitats (Gschweng et al. 2012). By contrast, our findings suggest that they are not tracking NDVI, as it increases uniformly over the rainy season in areas occupied by Eleonora's falcon. Instead, their spatiotemporal pattern appears associated with experience from previous years, with intra-individual home range overlap suggesting high site fidelity. This was especially evident based on overlap in home range during the same monthly period in consecutive years. The pattern of overlap provided a strong indication that falcons progressively move along the same areas year after year, selecting preferred habitat with regards to tree cover, habitat type, and elevation rather than chasing more productive areas.

To test our species–habitat associations we were able to map in high detail some of the activity areas of the species, showing that Eleonora's falcon actually uses more open habitats than what was indicated through the Madagascar vegetation mapping project, and that smaller fragments of certain habitat types may attract the individuals to spend time within a landscape. Our ground-truthing covered mostly areas occupied by tagged individuals during the first couple of months of their time in Madagascar, which corresponded with preferences for more open areas early in the season. These results support our assumption that before the rainy season begins they may hunt insect prey more easily in open areas such as grasslands and cultivations (Zefania 2001). In such places, single or scattered trees and forest patches are important for the perches they provide for roosting and resting in these open habitats (Cody 1985; Lihu et al. 2007), with more than 80% of the birds' time spent resting during the day or roosting at night.

The presence of Eleonora's falcons in fragmented landscapes might indicate that the species might cope with deforestation and land use changes, but in the long term the depletion of natural habitats could lead to overall depletion of the biodiversity of Madagascar, including of food resources for Eleonora's falcon as well (Kassara et al. 2017). The intensification of slash-and-burn and shortening of fallow cycles accentuates degradation and fragmentation of Madagascar's humid forests (Styger et al. 2007). Ongoing deforestation is rampant (Green and Sussman 1990; Harper et al. 2007), with Madagascar losing 21% of its tree cover from 2000 through to 2018 (Global Forest Watch 2019). With a clear preference for intact humid forest for much of the non-breeding season, such deforestation is expected to have a negative impact on the species.

In the present study, we managed to obtain detailed spatiotemporal data on Eleonora's falcon's wintering ecology including its daily activity patterns at an hourly rate, habitat usage during the day and at night, monthly patterns of progressive movements and associated changes in habitat preferences, as well as yearly and monthly fidelity. The extended distribution pattern of Eleonora's falcon in Madagascar and the remoteness of most of the sites at which the species occurs, impede the field-based study of their daily time budgets, as attempted for other raptors with comparatively much smaller wintering home ranges (Plumpton and Andersen 1997). Such studies typically also require a high number of field observers (Craig et al. 1988). Our work was possible primarily through the use of GPS–GSM–UHF loggers, with high spatial accuracy and high temporal frequency. These loggers provided us with the opportunity to associate environmental information with bird locations in remote areas, allowing for the detailed assessment of foraging frequency and night-time activity among other aspects of the species' wintering behavior. Field work was also of critical importance to assess habitat use, and in conjunction with telemetry and remote sensing data facilitated an integrative approach. Our findings, especially on the hourly and daily activity patterns, were nevertheless derived from small sample sizes and we encourage future work to complement our understanding of the wintering phenology of these long-distance migrants on their wintering grounds in a changing landscape.

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