University of Cyprus

DEPARTMENT OF BIOLOGICAL SCIENCES

BREEDING SUCCESS, WINTERING ECOLOGY AND MIGRATORY BEHAVIOUR OF ELEONORA’S FALCON (*Falco eleonorae* Géné, 1839)

DOCTOR OF PHILOSOPHY DISSERTATION

THOMAS G. HADJIKYRIAKOU

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THOMAS G. HADJIKYRIAKOU

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The present Doctoral Dissertation was submitted in partial fulfillment of the requirements for the Degree of Doctor of Philosophy at the ***Department of Biological Sciences*** *and was approved on the 24 May 2018 by the members of the* ***Examination Committee****.*

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The present Doctoral Dissertation was submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy of the University of Cyprus. It is a product of original work of my own, unless otherwise mentioned through references, notes, or any other statements.

ΠΕΡΙΛΗΨΗ

Το γεράκι της Ελεονώρας (*Falco eleonorae*) είναι μεταναστευτικό αρπακτικό το οποίο αναπαράγεται σχεδόν αποκλειστικά στη Μεσόγειο Θάλασσα, ενώ ξεχειμωνιάζει κυρίως στη Μαδαγασκάρη. Η γνώση γύρω από τις περιοχές διαχείμασης έχει πρόσφατα ενισχυθεί με τη χρήση δορυφορικών πομπών, μέσω των οποίων έχουν επίσης αποκαλυφθεί οι μεταναστευτικές διαδρομές. Παρόλα αυτά, δεν είναι ακόμη πλήρως κατανοητοί οι παράγοντες οι οποίοι επηρεάζουν τις επιλογές μετακίνησης και τη χρήση των διαφόρων βιότοπων που το είδος χρησιμοποιεί κατά τη μετανάστευση, αλλά και το χειμώνα. Η Κύπρος είναι το ανατολικότερο άκρο της εξάπλωσης του γερακιού της Ελεονώρας, περιοχή στην οποία είχε εκτιμηθεί παλαιότερα ότι έχει τη χαμηλότερη αναπαραγωγική επιτυχία, σε αντιδιαστολή με το δυτικότερο άκρο της εξάπλωσης του όπου η αναπαραγωγική επιτυχία έχει βρεθεί να είναι τριπλάσια από αυτή στην Κύπρο. Νέες τεχνολογίες επιτρέπουν σήμερα την παρακολούθηση των μετακινήσεων αυτού του μεσαίου μεγέθους αρπακτικού σε μεγάλη χωροχρονική λεπτομέρεια. Μια πλειάδα μέσων και τεχνικών είναι επίσης διαθέσιμη για τη μελέτη της αναπαραγωγικής οικολογίας του. Σε αυτή την εργασία μελέτησα την οικολογία του είδους καθ’ όλη τη διάρκεια του έτους, στις περιοχές αναπαραγωγής, τις μεταναστευτικές διαδρομές και τις περιοχές διαχείμασης.

Στην Κύπρο, χρησιμοποίησα μια ποικιλία μεθόδων, όπως καταμετρήσεις από τη ξηρά, τη θάλασσα και τον αέρα, χρησιμοποιώντας διάφορα εργαλεία όπως φωτογράφιση, φωτογραμμετρία και Γεωγραφικά Συστήματα Πληροφοριών για την εκτίμηση της αναπαραγωγικής επιτυχίας του είδους και την εκτίμηση της διαθεσιμότητας χώρων φωλεοποίησης, καθώς επίσης και για την εκτίμηση της επίδρασης που πιθανόν να έχουν τα φυσικά χαρακτηριστικά των θέσεων φωλεοποίησης στην αναπαραγωγική επιτυχία. Η αναπαραγωγική επιτυχία βρέθηκε να είναι στα ίδια επίπεδα με τον πυρήνα της εξάπλωσης του είδους, δηλαδή το Αιγαίο Πέλαγος, και ότι ο πληθυσμός είναι σταθερός όσον αφορά τον αριθμό των αναπαραγωγικών ζευγαριών. Με τη χρήση καμερών οι οποίες τοποθετήθηκαν σε φωλιές, επιβεβαίωσα για πρώτη φορά την ύπαρξη ενδοειδικής θήρευσης, με ένα θηλυκό άτομο να ταΐζει τους νεοσσούς του με νεοσσό που πηρέ από γειτονική φωλιά. Παρόλο που τέτοια συμπεριφορά είναι δύσκολο να επιβεβαιωθεί, πιθανόν να είναι κοινό φαινόμενο σε αυτό το κοινωνικό είδος, και η συχνότητα του να σχετίζεται με την πυκνότητα φωλιών και τη διαθεσιμότητα τροφής.

Χρησιμοποιώντας για πρώτη φορά σε αρπακτικό αυτού του μεσαίου μεγέθους, πομπούς GPS με ηλιακή φόρτιση, εντόπισα τις μεταναστευτικές διαδρομές ατόμων του είδους που φωλιάζουν στην Κύπρο. Συσχετίζοντας την ταχύτητα μετακίνησης και τη φυτοκάλυψη κατά μήκος των μεταναστευτικών διαδρομών, εντόπισα προτίμηση, ειδικά το φθινόπωρο, για περιοχές με μεγαλύτερη φυτοκάλυψη, πάνω από τις οποίες τα άτομα πετούν με μειωμένες ταχύτητες κατά τη διάρκεια της ημέρας, εξασκώντας τροφοληψία με ταυτόχρονη συνέχιση της πορείας τους. Τα άτομα κούρνιαζαν τα περισσότερα βράδια, συνδυάζοντας τροφοληψία σε σύντομους σταθμούς πριν και μετά τη διάσχιση οικολογικών εμποδίων. Αντίθετα, πετούσαν μέρα και νύχτα με μεγάλες ταχύτητες πάνω από μη κατάλληλα ενδιαιτήματα. Κατά την άφιξη τους στη Μαδαγασκάρη, τα άτομα από την Κύπρο, αλλά και την Ελλάδα τα οποία μελετήθηκαν μαζί, παρέμειναν σε σχετικά ανοικτά ενδιαιτήματα σε πιο χαμηλά υψόμετρα. Κατά τη διάρκεια του δεύτερου μισού της παραμονής τους στις περιοχές διαχείμασης, εντός της περιόδου των βροχών, μετακινούνταν προοδευτικά προς τα βροχοδάση σε πιο ψηλά υψόμετρα, αξιοποιώντας την αφθονία τροφής χωροχρονικά. Η δραστηριότητα τους, η οποία μελετήθηκε σε ωριαία βάση, αποκάλυψε ότι τα άτομα ξεκουράζονται ή κοιμούνται κατά το 80 % του χρόνου τους, ενώ τρέφονται για περίπου 15 % του 24-ώρου, σχεδόν αποκλειστικά κατά τη διάρκεια της ημέρας.

ABSTRACT

Eleonora's falcon (*Falco eleonorae*) is a migratory bird of prey that breeds almost exclusively in the Mediterranean Sea while spending the winter months primarily in Madagascar. Knowledge on its wintering grounds has been recently enhanced through the use of satellite telemetry, with which its migratory routes were revealed as well, but still, factors that affect migratory strategy and habitat usage both during migration and wintering are not well understood. Cyprus is the eastern limit of its breeding distribution, where it was thought to exhibit the lowest of breeding success rates, in contrast to the western limit, the Canary Islands, where breeding success was estimated to be three times greater. New technology and methods, presently allow the monitoring of the movement ecology of this medium-sized raptor in great spatiotemporal detail and an array of techniques are available for the study of its breeding ecology. In this work, I examined the year-round ecology of the species, at its breeding grounds, along migratory routes and at wintering areas.

In Cyprus, I used a diversity of methods with the incorporation of ground, aerial and boat surveys using photography, photogrammetry and GIS as tools for the estimation of the breeding success of Eleonora's falcon and for the assessment of nest site availability and the effect of nest site physical characteristics on breeding success. I found that breeding success is at the same level as at the core of its distribution, i.e. in the Aegean Sea and that the population is stable with regards to number of pairs. Using camera traps in nests, I confirmed for the first time between-nest intraspecific predation, witnessing a female feeding her nestlings with a nestling taken alive presumably from a nearby nest. Though such behaviour is rarely witnessed, it could be a common phenomenon in this colonial raptor whose frequency might be affected by fluctuations in breeding density and food availability.

Using solar-powered GPS-accuracy transmitters for the first time on this medium-sized raptor, I identified the migratory movements of Eleonora's falcon breeding in Cyprus. Relating the speed of travel with the vegetative cover along the routes, during day and night, I identified a preference, especially in autumn, for migration through vegetation-rich areas where tracked individuals flew with lower speeds during daytime, indicating fly-and-forage activity. Birds roosted during most nights, and added stopovers at selected sites before or after crossing ecological barriers. By contrast, they overflew unsuitable habitats at fast speeds both during the day and at night. Combining data from tracked individuals from Cyprus and Greece, I identified that upon arrival at the wintering grounds, the Eleonora's falcons first remained in relatively open habitat types at lower elevations. During the second half of the wintering season and well into the rainy season, they progressively moved towards areas at higher elevation covered with humid forest, utilizing food abundance in a geographically and temporally suitable pattern. Time budgets based on data obtained at an hourly rate revealed that falcons were inactive resting or roosting more than 80 % of their time, while forage takes just about 15 % of their daily time budget, and occurs almost exclusively during daytime.

This work is dedicated to

My wife Mary and our two children Kyriaki and Nikolas. This long-term study absorbed considerable amount of our family time for the last 8 years, which I hope to make up to them from now onwards.

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CHAPTER 1

Overview

Overview

"This is the best view I've ever seen in my life". When you hear that statement it is hard to believe that it is referring to birds feeding. Well it is, and hearing it from my ringing mentor, the late Alan Crabtree who spent his whole life working with birds and had seen so much all over the world, makes it even more inspirational. Watching a small group of Eleonora's falcons (*Falco eleonorae*) "dancing" at dusk, while feeding on the wing on *Anoxia baraudi* beetles besides Akrotiri village, with the salt lake in the background, was indeed beautiful. That was the first night I handled Eleonora's falcon and looking at them in the eyes further inspired me to uncover their life history secrets.

Annual cycles and migratory connectivity

The stages of the annual cycle of animals, irrespective of the spatial scale at which they occur, are interlinked (Webster et al. 2002; Marra et al. 2015). Migratory species can exploit areas thousands of kilometres apart; yet, events in one of these geographically distinct areas can affect subsequent stages of their annual cycle (Webster et al. 2002; Marra et al. 2015). For example, in American redstarts, intraspecific competition for securing optimal wintering habitat has been found to have an effect on timing and condition of arrival at the breeding grounds, subsequently affecting their breeding success (Marra et al. 1998). Migratory behaviour exists in most groups of living organisms following seasonal changes (Berthold 1991) and it has been attracting interest since Aristotle (384 – 322 BC) (Balme and Gotthelf 2002). But because of their mobility, birds have, perhaps more than any other taxonomic group, the unique capacity to select habitat to satisfy their daily and seasonal requirements (Cody 1985). Thus, habitat selection is a continuous process for migrating birds, whether on breeding grounds, within migrating corridors, or at their wintering quarters, and this occurs at different temporal and spatial scales (Cody 1985), during which birds must make critical decisions (Kerlinger 2008). Nevertheless, site fidelity in adult migrants suggests that these critical choices might be taken primarily during the first year of the life of each individual and upon survival they stick to their successful pattern (Cody 1985), exhibiting outstanding navigational capacity (Berthold 2001) with the use of several types of compasses, including the sun, the stars, and magnetic fields (Alerstam 1993). Out of about ten thousand bird species on Earth, about four thousand migrate (Bildstein 2006), and these can be classified as complete, partial or eruptive migrants based on the proportion of the population that migrates, and on whether migratory patterns are predictable or not (Kerlinger 2008). Bird migration has two major driving forces; birds move to lower latitudes during autumn to enhance their winter survival chances, while in spring they move to higher latitudes where they can achieve higher reproductive success (Newton 2016). Migration involves tens of millions of birds of prey (Bildstein 2006), but in spite of migration dating back 55 million years, it is still flexible and can appear and disappear over decades in raptor species (Bildstein 2006). In order to assess the conservation status of a species, bearing in mind the connectivity between annual cycle stages and the spatiotemporal autocorrelation which guides decisions within a population (Cresswell 2014), a comprehensive examination of its annual cycle is necessary (Marra et al. 2015), including at breeding grounds, on migratory routes and in wintering areas (Sillett and Holmes 2002). Breeding success studies are an important aspect of population ecology in birds (Green 2004; Steenhof and Newton 2007), and have been found to contribute more to population changes compared to wintering factors (Cresswell 2014), and the breeding success of a raptor population reflects its overall population health (Brown 1974).

Eleonora's falcon life history, ecology and biology

The genus *Falco* belongs to the subfamily *Falconinae* of the *Falconidae* family, which comprises 39 species (Del Hoyo et al. 1994). Eleonora's falcon is closely related to sooty falcon (*Falco concolor*) and Eurasian hobby (*Falco subbuteo*), all three of them belonging to the subgenus Hypotriorchis (Seibold et al. 1993; Helbig et al. 1994; Wink and Sauer-Gürth 2000). Eleonora's falcon was described in 1839 by Géné (Vaughan 1961) and named after Eleonora of Arborea, Princess of Sardinia, who published a set of laws providing protection for falcons. Eleonora's falcon was unknown during her times, since Princess Eleonorae passed away in 1403, but nevertheless, the species was named in honor of her efforts towards the protection of falcons (Walter 1979).

Eleonora's falcon is a medium-sized raptor (36 – 42 cm length, 90 – 105 cm wingspan), exhibiting reverse sexual dimorphism as in many raptor species (Wheeler and Greenwood 1983), with an average weight of 327 ± 22 g for males and 399 ± 27 g for females (Ristow and Wink 1985; Del Hoyo et al. 1994; Wink and Ristow 2000). Also, it is a colour-polymorphic species with light and dark morphs, a melanin-based polymorphism maintained by Mendelian inheritance, with dark allele been the dominant one (Ristow et al. 2000). Sexual maturity is reached at the age of 2 years for males and 3 years for females (Ristow et al. 1983), rarely earlier (Ristow et al. 1989). The oldest known individual in the wild was 16 years old (Ristow et al. 1989). The identification of adult males and females can be based on cere and eye-ring color, with males having orange-yellow and females bluish-green ones (Walter 1979; Wink and Ristow 2000; Gangoso et al. 2011) (Fig. 1).

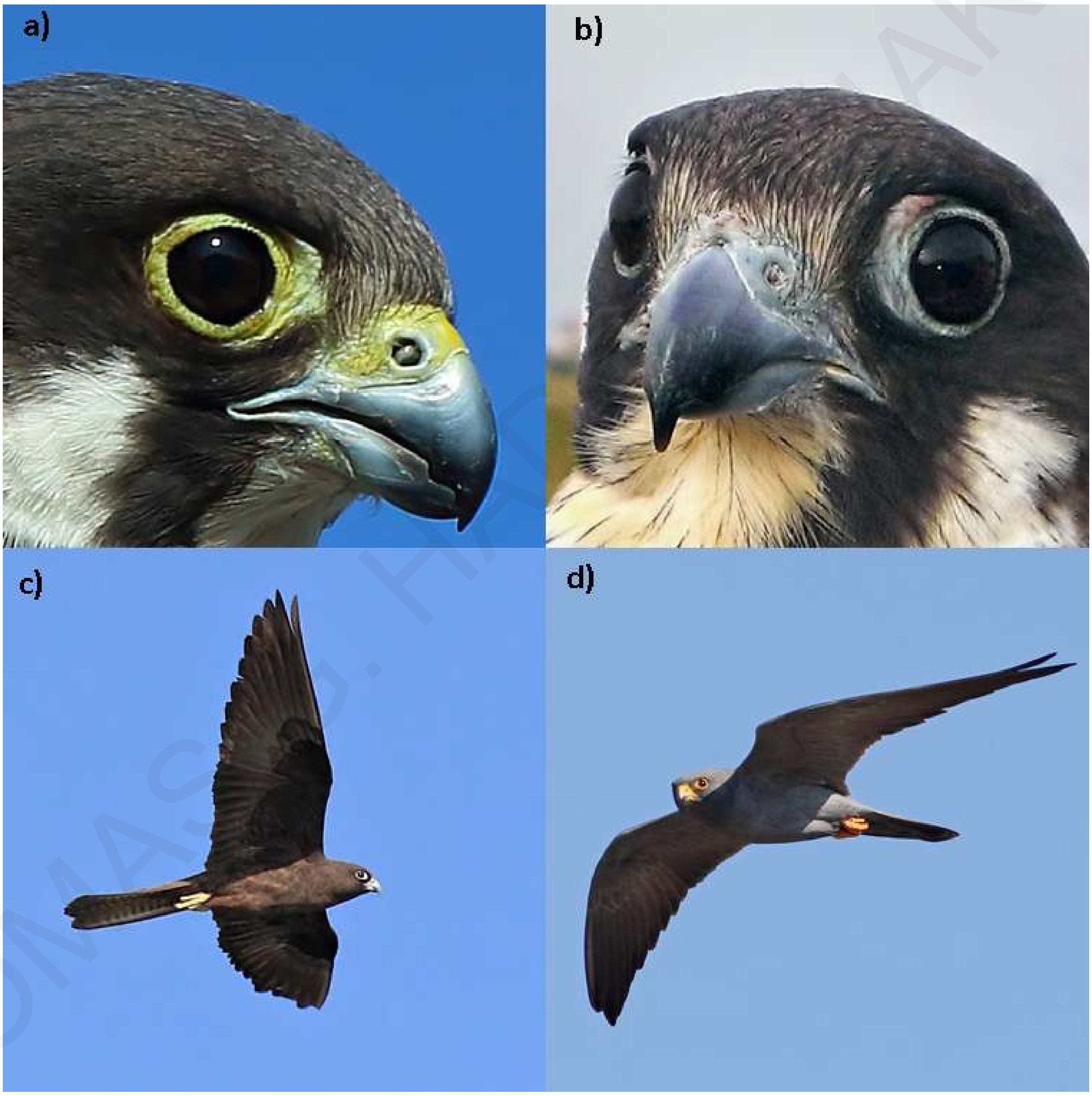

Figure 1: a) Eleonora's falcon adult male light morph (Cyprus); b) Eleonora's falcon adult female light morph (Cyprus); c) Eleonora's falcon adult male dark morph (Cyprus), d) Sooty falcon adult (Madagascar).

Eleonora’s falcon is a long-distance migratory raptor, which migrates from the breeding grounds mostly in the Mediterranean Sea, to Madagascar in the Southern Hemisphere (Bildstein and Bird 2007). It breeds in the Mediterranean and the Atlantic, from Cyprus in the east to the Canary Islands and the Atlantic coast of Morocco in the west (Walter 1979), but the majority of breeding pairs are found on islands and islets in the Aegean Archipelago (Walter 1979). It overwinters almost exclusively in Madagascar (Kassara et al. 2017), though immatures and other non-breeding individuals can be found quite far from breeding and wintering grounds, over much of Africa and Europe, but not north of the Alps (Walter 1979). Satellite telemetry data have recently confirmed that most individuals overwinter in Madagascar after crossing the African continent (Gschweng et al. 2008; López-López et al. 2009; López-López et al. 2010; Kassara et al. 2012; Mellone et al. 2013). Eleonora’s falcon and sooty falcon may overwinter in Madagascar to exploit ecological niches not shared with other insectivorous falcons overwintering in southern Africa (Alerstam 1993).

Eleonora’s falcon is a monogamous and social species breeding in colonies ranging from a handful up to a few hundred pairs (Walter 1979; Ristow 2004). Breeding sites are typically remote and isolated coastal cliffs along migratory routes of small birds (Del Hoyo et al. 1994). Nests are situated on sea cliffs and on top of inaccessible and protected islets, in sheltered points, holes, crevices and ledges (Fig. 2), or even under bushes (Walter 1979), while eggs are laid directly onto the ground without any material underneath (Walter 1979). Distances among and densities of nests vary between colonies, depending on the terrain, with adjacent nest sites selected so that there is no visual contact between them (Walter 1979). Nest spacing is typically 20 – 50 m but distances as small as 2 m have been recorded (Ristow and Bourdakis 1999). Nest depth usually ranges between 25 cm and 2 m (Walter 1979). Nest site quality is an important factor determining breeding success, with inferior nests more likely to be abandoned and not re-used in successive years, while well-established nest sites are used year after year (Clark and Peakall 1977). Eleonora’s falcon breeds later in the calendar year than any other migrant breeding bird in Europe (Dimalexis et al. 2008). At the end of the breeding season, all individuals depart the breeding grounds, most by the end of October and all by mid-November (Walter 1979), and they return to the breeding grounds between early April and May (Walter 1979).

Figure 2: Eleonora’s falcon nestling in an exposed ledge at Episkopi colony, Cyprus

The species exhibits strong site tenacity with adults using the same territory year after year, while young birds are thought to nest close to their natal grounds (Swatschek et al. 1993; Ristow and Bourdakis 1999). Following the return to breeding grounds from April, territories are occupied and intensive courtship starts in July (Ristow and Wink 1995; Ristow and Bourdakis 1999), while egg laying takes place from mid July to early August. One to four eggs are laid (Del Hoyo et al. 1994) at intervals of 2 – 3 days (Walter 1979), with incubation lasting about 28 – 33 days, undertaken typically by the female parent (Walter 1979; Del Hoyo et al. 1994). Most nestlings hatch during the last week of August while fledglings are airborne after 37 days (Walter 1979; Del Hoyo et al. 1994). The departure from the colonies towards wintering grounds occurs about 2 – 3 weeks later when fledglings are 55 – 60 days old (Del Hoyo et al. 1994), while nests are completely deserted by mid-November (Ristow and Bourdakis 1999). Breeding success has been described as ranging from 2.6 offspring per breeding pair in Morocco, to 0.8 in Cyprus (Walter 1979; Walter and Foers 1980). Egg losses can be as high as 43% and nestling losses up to 10% (Ristow and Bourdakis 1999).

Eleonora's falcon feeds on large insects throughout the year and switches its diet to small passerine birds during the nestling raising period (Walter 1979). Upon arrival at their breeding grounds individuals still feed on large flying insects (e.g. Lepidoptera, Coleoptera, Odonata, and Orthoptera), during which time they might travel over continental land or other islands where they might find an abundance of insects, for instance over wetlands and other insect-rich habitats (Del Hoyo et al. 1994; Mellone et al. 2013), while partial feeding on spring migrants might also occur (Walter 1979; Del Hoyo et al. 1994). When postnuptial passerine migration begins, and nestlings of Eleonora's falcon have hatched, there is a gradual switch to foraging on birds until they become completely ornithophagous (Clark 1974; Walter 1979; Delaugerre et al. 2012). They feed on a variety of birds, with about 100 species recorded thus far, ranging in size from willow warblers to turtle doves (Walter 1979), with prey typically weighing 10 - 30 g (Ristow and Bourdakis 1999). The frequencies with which species are caught likely relate more to occurrence rates rather than on any actual preferences for certain prey species (Walter 1979). Indeed, they breed on islets and at coastal cliffs so they can intercept the stream of passerine migrants over the sea where they can more easily catch them (Clark 1974). They have been observed actively flying away from the colony over sea at altitudes > 1000 m (Rosén and Hedenström 2002) and up to 5000 m or even more (Rosen et al. 1999). This is consistent with data from radar studies showing that passerine passage migrants fly at a mean altitude of 1500 m to 3000 m and even up to 4500 m (Rosen et al. 1999). They usually hunt crepuscularly and it was suggested that they have considerable night foraging activity as well (Walter 1979; Del Hoyo et al. 1994; Buij and Gschweng 2017), adapting their feeding spatiotemporal pattern to reflect the bird migration patterns in the vicinity of the colony (Walter 1979). The male is usually the provider and the female takes care of the nestlings until they are at least two weeks old, when the female can then hunt as well (Walter 1979). Feeding in the Mediterranean colonies takes place predominantly at dawn and early morning hours, although this depends on the timing of bird migration pulses in the wider area of the colony. By contrast, in the Atlantic colonies hunting may continue throughout the day (Walter 1979).

Conservation status

The Eleonora's falcon's global population is estimated at about 15000 breeding pairs (Walter 1979; BirdLife International 2017; Touati et al. 2017), of which approximately

80% breed on islands in the Aegean Sea (Dimalexis et al. 2008). The species is classified as Least Concern at a global level (BirdLife International 2015), however it is included in Annex I of the EU Directive 2009/147/EC and thus requires special conservation measures to ensure its survival and reproduction (European Parliament 2009). In Cyprus, Eleonora's falcon is protected under the National legislation of the Republic of Cyprus (N.152(I)/2003) and under the relevant legislation of the British Sovereign Base Areas (SBA's) of Cyprus, implementing locally the provisions of the European Birds' Directive 2009/147/EC. All nesting cliffs in Cyprus are protected as Natura 2000 sites (Zaggas et al. 2009; SBAA 2015).

The Cyprus population

Cyprus is the easternmost limit of the breeding range of Eleonora's falcon, isolated by at least 560 km from the closest breeding colony in the Aegean Sea (Vaughan 1961; Walter and Foers 1980). In Cyprus, breeding colonies are patchily distributed between Cape Gata and Cape Aspro on the south coast of the island (Flint and Stewart 1992). The first breeding records for Cyprus were of a few pairs at Cape Gata at Akrotiri on 8th May 1875 (Lilford 1889). There was an annual ringing project between 1961 and 1970 in Cyprus, when a total of 123 nestlings were ringed (Flint 1971), providing some of the first data for migration of the species to Madagascar. Indeed, one of the first confirmed records that birds from their breeding grounds are migrating to Madagascar for wintering, was a nestling ringed in Cyprus that was shot in Madagascar in 1962, about 50 days after its departure from Cyprus, indicating that it took this individual less than 50 days to travel from Cyprus to Madagascar, a straight-line distance of 6,000 km (Walter 1979). Previous breeding success estimates of 0.8 – 1.0 fledglings per breeding pair at Akrotiri and Episkopi (Walter and Foers 1980), compared to 2.6 fledglings per breeding pair at Morocco (Walter 1979), indicated that there might be an eastward decreasing trend in breeding success of Eleonora's falcon (Xirouchakis et al. 2012). Such low breeding success levels of the breeding population in Cyprus might lead to population decline (Ristow and Wink 1985; Gschweng et al. 2011), because at least 1.2 fledglings per breeding pair are considered necessary to ensure colony sustainability (Ristow and Wink 1985).

Research hypotheses

For my PhD research, I particularly focused on the ecology of the breeding population of Eleonora's falcon in Cyprus. I also collaborated with research groups focusing on other populations in the breeding range to combine our efforts towards a study on the wintering period in Madagascar (Kassara et al. 2017), with close cooperation with the Animal Biodiversity & Evolutionary Ecology Group of the Department of Biology of the University of Patras, and the Hellenic Ornithological Society. My thesis research projects were thus divided between studies of the breeding, migration and wintering periods of Eleonora's falcon, focusing on factors affecting breeding success, migration behaviour, and wintering habitat use respectively:

- **Breeding success – Chapters 2 and 3**
  The presumed non-sustainable low breeding success of Eleonora's falcon breeding in Cyprus (Walter 1979; Ristow and Bourdakis 1999) triggered my interest to investigate it further. I used a variety of methods combining cliff-top, boat and drone surveys, photography, videography and photogrammetry, to comprehensively assess breeding success through all its progressive stages (Green 2004; Thorup et al. 2010), testing if the previous breeding success estimates are still true, as well as if specific nest site physical factors affect breeding success (Chapter 2). Specifically I tested the sustainability prospects of three colonies in Cyprus. As part of this work, I installed camera traps, to monitor nest ecology and nestling growth and parental care (Green 2004) and had the opportunity to witness behaviour recorded for the first time in raptors, such as non-parental infanticide (Chapter 3 and Appendix 1, Hadjikyriakou and Kirschel 2016). Cannibalism is common in animals (Polis 1981), but relatively infrequent in birds (Mock 1984), yet for colonial species such as some falcons I hypothesise it might indeed be more frequent than had been anticipated, especially in cases where breeding densities are high (Polis 1981) and there is a shortage of food (Gangoso et al. 2015).

- **Migratory behaviour – Chapter 4**
  Utilizing GPS loggers as well as PTT transmitters, I aimed at identifying the migratory routes of the birds breeding in Cyprus (Chapter 4). Telemetry data are unbiased, with measurable accuracy levels and thus track the movement of individuals effectively (Williams et al. 2017). Although the presence of species on breeding and wintering grounds makes up much of their annual cycle and thus

research is usually biased towards those areas, spatiotemporal movement patterns during migration are equally important (Jacobsen et al. 2017). Therefore in this study, I tested the hypothesis that Eleonora's falcon migratory routes in autumn and spring favor habitats with rich vegetation, which offer refueling opportunities, either through fly-and-forage or by spending time at selected stopover sites (Thorup et al. 2017). Furthermore, I compared migratory strategy between seasons, determining the speed travelled over different habitats during the day and at night.

- **Wintering phenology – Chapter 5**
  Finally, I studied the spatial distribution, phenology and daily activity cycles of Eleonora's falcon at their wintering grounds, combining data from transmitters I deployed, with data from transmitters attached by collaborators in Greece (Chapter 5) and elsewhere throughout the breeding range (Kassara et al. 2017; Appendix II), aiming at identifying critical components of the wintering ecology (Tottrup et al. 2012). To this end, the high positional accuracy and dense temporal collection pattern of the transmitters used in this study highly enhanced the usefulness of data collected, allowing for fine scale analyses to be conducted to hourly pattern detail, while field work in Madagascar provided further evidence of their wintering ecology and the threats they face at their wintering grounds (see Fig. 3).

This comprehensive study of the annual cycle of Eleonora's falcon breeding in the Eastern Mediterranean can advance our current knowledge on the ecology of the species. The use of novel survey techniques and state of the art individual tracking devices, provided us with fine details of the species yearly cycle, including its breeding success, autumn migration, wintering phenology and spring migration on the way back to breeding grounds. Being the first study of its kind providing such detailed analysis, we consider the results produced of crucial importance for the advancement of the current knowledge of the species, but also potentially for many other species with similar behaviour or occupying the same habitats. The results of this study also allowed evaluation of the threats and pressures on this long-distance migratory species, at different parts of the world, separated between them by more than 7000 km.

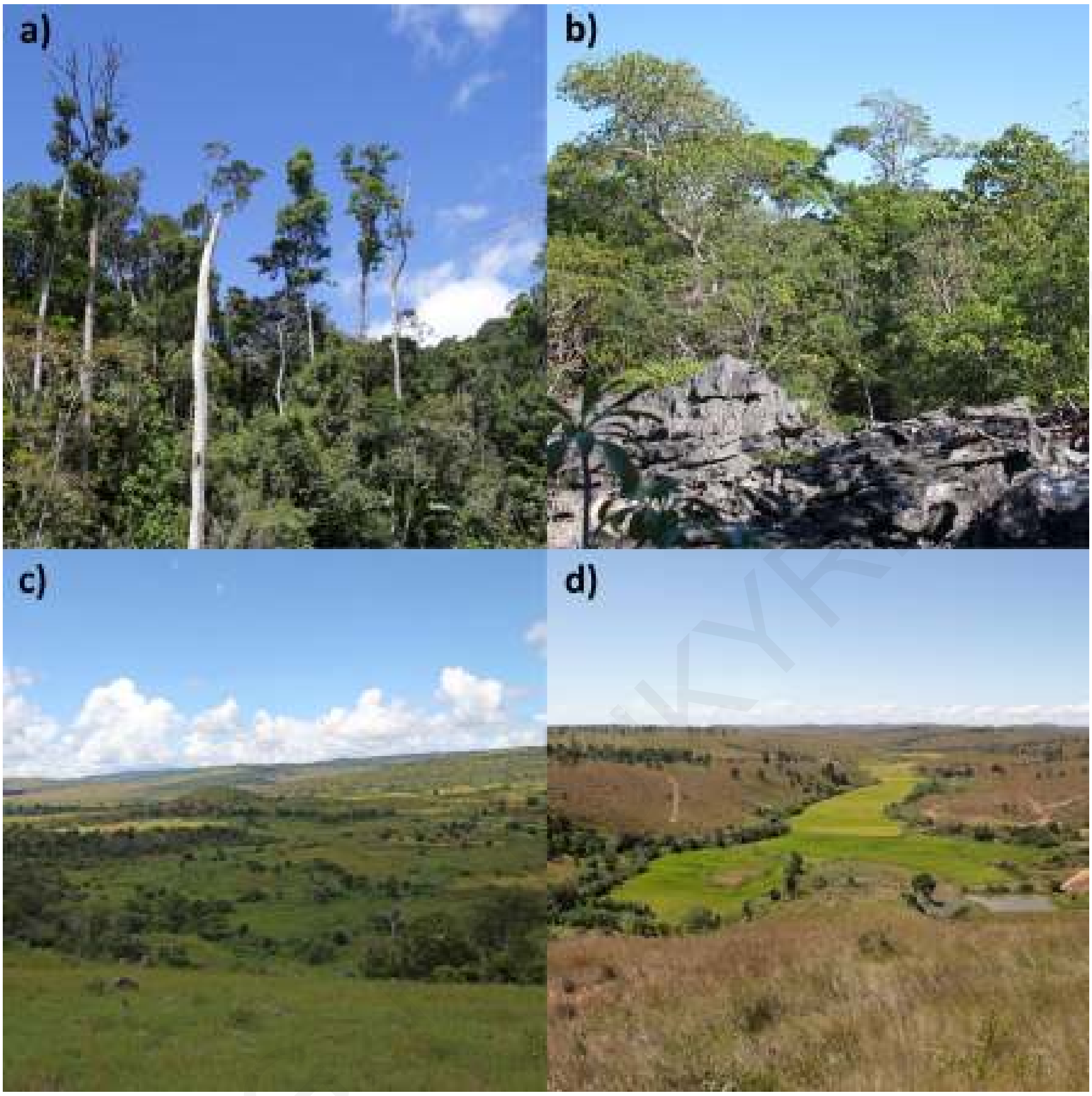

Figure 3: Habitat types in Madagascar; a) humid forest; b) western dry forest; c) grassland with scattered trees and western dry forest remnants and d) rice field, grassland / eucalyptus plantations.

CHAPTER 2

Using boat surveys, drones and photogrammetry to appraise breeding success and the factors influencing it in Eleonora's falcon

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ABSTRACT

Early estimates of the breeding success of Eleonora's falcon (*Falco eleonorae*), suggested that Akrotiri colony in Cyprus had the lowest breeding success among all the colonies throughout the species' breeding range, at a level seemingly unsustainable, suggesting the colony may be in danger of gradual extinction. Here we use a diversity of methods with the incorporation of photography and photogrammetry, to reassess the breeding success and the effect of nest characteristics on the Eleonora's falcon breeding population in Cyprus. We found that breeding success is 1.54 ±0.85 fledglings per breeding pair, which is higher than previous estimates and compares favourably with the estimates for the core of the species breeding range, the Aegean Sea in Greece. In addition, by analyzing breeding temporal variation and nest characteristics, we found that early breeders and reused nests offer prospects for higher breeding success, while physical nest characteristics have a limited effect on colony productivity. Threats on Eleonora's falcon in Cyprus were thus not related to nesting sites as such, but to human activities and land management practices inland at feeding and ranging grounds.

Keywords: Cyprus, Digital Surface Model, sea cliff, raptor, fledgling, photography.

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INTRODUCTION

Eleonora's falcon (*Falco eleonorae*) is a social raptor with a total population of approximately 15000 breeding pairs (Walter 1979; BirdLife International 2017; Touati et al. 2017), breeding primarily on islands and islets in the Aegean Sea (Dimalexis et al. 2008). The breeding population though ranges from Cyprus in the east, westwards across the Mediterranean Sea, the Atlantic coast of Morocco and the Canary Islands (Walter 1979), in colonies ranging from a few pairs up to a few hundred pairs (Vaughan 1961; Walter 1979). Colonies are irregularly distributed and typically located on remote and isolated coastal cliffs and islets along migratory routes of small passerines (Vaughan 1961; Walter 1979; Del Hoyo et al. 1994), facilitating Eleonora's falcon, which otherwise feeds on large (over 10 mm long) insects throughout the year, to gradually switch its diet to small (up to about the size of turtle dove) migrating birds during the nestling raising period to cope with increasing energetic nestling requirements (Walter 1979). Although nest sites on coastal cliffs are relatively scarce and exposed to winds, breeding pairs prefer to nest there rather than further inland where disturbance and predation are inevitable (Walter 1979; Urios and Martínez-Abraín 2006).

Presence of Eleonora's falcon at the breeding grounds is typically between April and November (Walter 1979). The species has been found to exhibit strong site tenacity (Ristow and Bourdakis 1999), and the isolation of the Cypriot population at the eastern extreme of the breeding range might have resulted in restricted gene exchange with other colonies (Swatschek et al. 1993) as well as low immigration levels (Wink et al. 1987; Gschweng et al. 2011). While breeding success is just one parameter of species demography (others being mortality, emigration and immigration), it is generally thought to be the most critical one (Steenhof and Newton 2007). For a complete estimate of breeding success, surveys should include all the stages of breeding, including territory occupancy, egg laying, incubation and number of nestlings hatched and fledged (Brown 1974). However, when conditions do not allow for such systematic fieldwork, as in the case of cliff-nesting species, field surveys should focus on the most critical breeding stage, i.e. the number of nestlings that reach fledging age (Steenhof and Newton 2007). For Eleonora's falcon, nestling mortality has been estimated at about 10% in the first 2 weeks, while thereafter mortality is negligible (Ristow and Bourdakis 1999). Therefore, based on breeding timing estimates, the number of nestlings counted from mid-September onwards can be considered a sufficient estimate of the number of fledglings (Ristow and Bourdakis 1999). Previous breeding success estimates of 0.8 – 1.0 fledglings per breeding pair at Akrotiri and Episkopi (Walter and Foers 1980), compared to 2.6 fledglings per breeding pair in Morocco (Walter 1979), indicated that there might be an eastward decreasing trend in breeding success of Eleonora's falcon (Xirouchakis et al. 2012). Such low breeding success levels of the breeding population in Cyprus might lead to population decline (Ristow and Wink 1985; Gschweng et al. 2011), because at least 1.2 fledglings per breeding pair are considered necessary to ensure colony sustainability (Ristow and Wink 1985). Also the migrant birds pulse over breeding areas in Cyprus restricts feeding opportunities time-wise, to a relatively small dawn to early morning window, further increasing the concerns of decline (Walter 1979) of a population which is already under pressure. Apart from food availability, nest sites are a limiting factor in the assessment of the potential of population increase in raptors (Danchin and Wagner 1997; Newton 2010b). In other Eleonora's falcon breeding colonies, physical nest characteristics were found to affect breeding success (Touati et al. 2017). Even for social raptors, such as the Eleonora's falcon, nest sites are limited by topography and predation / disturbance potential, and determined by the existence of suitable nesting positions (e.g. ledges, holes and crevices). Therefore, small nest groups are usually found on stretches of sea-cliff faces (Walter 1979).

In this study we re-evaluated the population status and the breeding success of Eleonora's falcon breeding in Cyprus and assessed the factors affecting it, combining boat, ground and aerial surveys, with photography and photogrammetry. Breeding colonies in Cyprus are located on the southern coast of the island, from Cape Gata to Cape Aspro (Flint and Stewart 1992). We studied all the breeding colonies of the island (Fig. 1), with particular attention to the Akrotiri colony, which hosts about 30 pairs (Hadjikyriakou and Kirschel 2016) and comprises the intensively study area (Postupalsky 1974). Eleonora's falcon is included in Annex I of the EU Directive 2009/147/EC and thus requires special conservation measures to ensure its survival and reproduction (European Parliament 2009). It is protected through legislation in the Republic of Cyprus (N.152(1)2003) and the Sovereign Base Areas (SBAs) of Cyprus (Ordinance 21/2008), both of which host breeding grounds of the species exclusively in designated areas of the Natura 2000 network of the island (Zaggas et al. 2009; SBAA 2015).

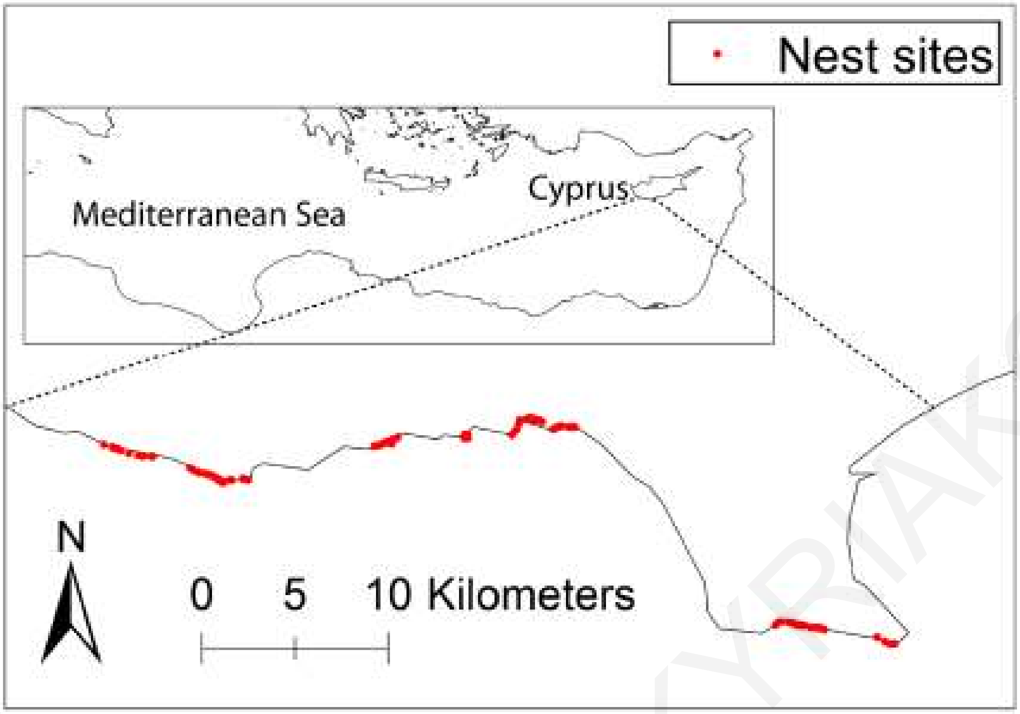

Fig. 1: Study area at the southern coast of Cyprus (map boundaries drawn from European Commission 2015), with nesting sites comprising the three colonies of Cape Aspro, Episkopi and Akrotiri (from left to right).

MATERIAL AND METHODS

Population counts

Population counts were conducted primarily through boat surveys, with the exception of a cliff section for which boat access was precarious due to shallow waters, whilst there was land access from the base of the cliff. All population counts were completed during the nestling raising period to be combined with the breeding success work. Three boat-trips, one per each colony in Cyprus (Akrotiri, Episkopi and Cape Aspro), were organised each year for six consecutive breeding seasons (2012 – 2017). Surveys were conducted between 06:00 – 11:00 hours, counting all the adults seen either flying or perching. The hunting window for Eleonora's falcon in Cyprus is quite small (Walter 1979), thus we assumed that the occurrence of falcons around the cliffs is a strong indication of population size. This would especially apply during the nestling-raising period, when females are typically guarding the nests and males go on short hunting excursions during the early morning hours, returning with prey, which they pass on to the females (Walter 1979). We aimed to perform counts from a distance about equal to the cliff height with boat speed 2-4 knots/h (Dimalexis et al. 2008), while slowing down and completely stopping to record breeding success data. We analyzed population counts data with TRIM software (Pannekoek et al. 2006), using linear trend modelling with software imputed values for missing years. Estimation of the actual number of breeding pairs was based on the methodology proposed by (Dimalexis et al. 2008), who used the number of adults counted, and adjusted it by multiplying by 0.7 to get an estimate of the number of breeding pairs in Greece. In Dimalexis et al. (2008) study, some nests were further inland, which was not the case in Cyprus, so we used an adjustment factor of 0.6 instead, to reflect the better view of the breeding colonies from the boat in Cyprus. In addition to this method, we used alternative approaches related to the number of nests detected and breeding success estimates. Specifically we used a nest detection factor of 90 %, 80 % and 25 % for Akrotiri, Episkopi and Cape Aspro colonies respectively (Walter and Foers 1980), as well as the relation between the number of adults counted and the number of breeding pairs we recorded during the intensively studied Akrotiri survey in 2013, to extrapolate number of breeding pairs for the other colonies and seasons.

Breeding success

For the estimation of breeding success, we recorded all active nests identified during the population count surveys between 2012 and 2017. Surveys were organised during the nestling raising period, concentrated around the last week of September when the nestlings were old enough to leave the nest scrape and became more visible, but had not yet fledged (Walter 1979). For each active nest with nestling(s) spotted, using a protocol modified from HOS (2012), we recorded nest characteristics and bird related information. These included trip details, weather conditions, nest type (exposed ledge, deep ledge, hole, crevice and under bush), nest aspect (N, NE, E, SE, S, SW, W, NW), cliff inclination (in bands of 10 degrees), visibility within the nest (scale from 1 – 3), remote nest mapping information (GPS location, bearing, distance and angle of observation), as well as nestling and pair presence and activity (Walter 1979; Xirouchakis et al. 2012). All the nests were photographed for further examination to enhance data accuracy (Clark 2007) and to estimate nestling age by comparing the development of each nestling with the daily video footage from two camera traps installed during the 2013 breeding season (Hadjikyriakou and Kirschel 2016) which covered the entire breeding season. This way, we were able to estimate nestling age within an accuracy of three days and consecutively calculated laying, hatching and fledging dates, based on the duration of each breeding stage observed from cameras, as well as on the literature (Walter 1968; Walter 1979; Dawson 2004). Using a GPS to directly map nest positions (López-Darias and Rumeu 2010) was not possible. Alternatively, we remotely calculated nest coordinates and nest height by initially calculating the horizontal distance from the observer to the nest, using the direct distance and angle taken using a laser rangefinder (at this stage we calculated nest height as well) and then calculating the shift in coordinates from the observer's position based on the horizontal distance and the bearing taken using a compass. For the core study area, i.e. the Akrotiri colony, we undertook additional surveys (about four in each season), from the boat and the cliff top for those nests visible from there, to monitor in more detail the breeding success progress. To be more efficient in finding the nesting cliffs, we undertook cliff-top surveys in July and August 2012, along a transect covering the entire length of Akrotiri cliffs recording positions of all adults seen with a handheld GPS.

Furthermore, for the 2013 season, we studied the breeding stages at Akrotiri colony from nest occupation to egg laying, hatching and fledging, to identify possible between-stage losses (Postupalsky 1974; Steenhof and Newton 2007; Thorup et al. 2010). Akrotiri is considered the most suitable colony in Cyprus for such systematic work (Flint 1972) because cliffs are relatively low and many nests can be monitored from the cliff top as well. For each breeding stage we used a variety of methods following Andersen (2007):

- Territory occupancy was estimated early in the breeding season through cliff-top and boat surveys, recording pairs around nest sites or territorial activity of one partner (Walter 1979; Steenhof and Newton 2007).
- Clutch size per nest was recorded from the cliff top, but for most nests this was not possible. This was not feasible from a boat either, because nests were on steep sea cliffs high up and visibility within the nest from a convenient angle was not possible (Bibby 2000; Steenhof and Newton 2007). Hence, in addition to cliff-top counts, during the second week of August when most pairs had laid their eggs but had not yet hatched (Wink et al. 1993; Xirouchakis et al. 2012), we used a small custom-made drone (quadcopter) equipped with a GoPro camera (Hero 3 black edition). The drone would take off and be operated from a boat and approach nests using wirelessly transmitted live view, getting photo and video footage, which was examined later to count number of eggs in each nest. Highest possible photo and video resolution was used to enhance egg identification (12 MP images and 1440p video resolution at 24 frames per second). Every effort was undertaken to take the footage as quickly as possible and to minimise any disturbance, with most flights lasting less than 5 minutes and keeping distance to nests at over 10 m (Vas et al. 2015; Radiansyah et al. 2017). Adult birds would, upon drone approach, move away from the nest and return a few minutes after its withdrawal, allowing in the meantime sufficient time for nest recording.
- Counts of eggs hatched were undertaken during the first week of September when most nestlings were expected to have hatched (Xirouchakis et al. 2012). These were performed via boat and cliff-top surveys using binoculars and telescopes. All nests were photographed to enhance data collection accuracy.
- Number of nestlings fledged was recorded through boat and cliff top-surveys. These surveys concentrated within the period when nestlings were at least two weeks old, since mortality after that age is thought to be negligible and nestling numbers at that age are consistent with fledgling numbers (Clark 1974; Ristow and Bourdakis 1999; Steenhof and Newton 2007).

Nest site selection

Nest site preferences were evaluated using a Digital Surface Model (DSM) of the Akrotiri cliffs, which was created with photogrammetric techniques. DSM in conjunction with GIS is a powerful combination for the prediction of the presence of species (Guisan and Zimmermann 2000). Akrotiri cliffs stretch for about 10 km and elevation ranges from sea level to 60 m above sea level. Two sets of low oblique overlapped photographs of the cliff face were taken during two flights with a Cessna plane, using a Canon EOS 40D camera body and a zoom lens (EF70-200mm f/2.8L IS II USM), from a distance of about 100 m and flight heights of about 100 m and 200 m respectively. Photographs were processed with Agisoft's Photoscan software using GNSS control points acquired on site (Skarlatos et al. 2013). The final photogrammetric products were an orthophotograph of the study area with a pixel size of 0.5 m and a DSM with 0.5 m. It should be noted that the cliff model created by the software is a full 3D model of the area, but the exported DSM reduces the 3D model to a 2.5D model, losing information (Mikhail et al. 2001). This is particularly important when the area of interest has steep and vertical slopes (Mikhail et al. 2001). The target cliff area was isolated using the subsequently created contour map, where the top and bottom of the cliffs could be identified and a polygon was selected to limit the Area of Interest (AOI) to the cliff area only. The DSM was imported into ArcGIS (ESRI 2012) and downsampled to a pixel size of 2 x 2 m for further processing, because this size is ecologically meaningful for the birds within the context of this study. Within the GIS environment, elevation, inclination and aspect of each pixel were calculated. We used the information obtained from each nest, i.e. cliff inclination, nest aspect and nest elevation from the six-year surveys of nests at Akrotiri colony and the DSM was queried to assess suitability of the cliffs. Highly suitable was considered as the area of the cliff falling within 1 standard deviation of the mean from the mean values of the nests for each of the three DSM parameters, i.e. elevation, inclination and aspect.

Factors affecting breeding success

We investigated which physical nest characteristics influence breeding success, and if temporal distribution of egg laying has any relevant effect, with the use of a zero truncated Poisson regression model (StataCorp 2013). Specifically, we tested for the effect of laying date, cliff inclination, nest type, nest aspect and nest elevation on fledgling numbers of successful pairs. Together with those variables we tested for the effect of colony, as well as any possible contribution of rainfall during the pre-breeding season. Precipitation is related to insect abundance (Wolda 1978; Wolda 1988), which in turn affects clutch size (Ristow 2004; Steenhof and Newton 2007), because females feed predominantly on insects during the egg formation stage (Walter 1979), with well-fed females producing more eggs (Wink et al. 1980). We used Akaike's Information Criterion (AIC) to select the best fit model. We similarly ran zero truncated Poisson regression analysis for the intensively studied colony at Akrotiri as well, for each of the three breeding stages, i.e. eggs laid, eggs hatched and hatchlings fledged. We also tested for a correlation between nest usage frequency and number of fledglings using Spearman correlation coefficient.

RESULTS

Population counts

We counted a mean 232 (SD = 14.00, N = 6) adults per season (Fig. 2) and we found that the population size was stable over the six years (Wald-test (1) = 1.68, P = 0.195). Population size remained stable even when including previous counts back to 2000 (Wald-test (1) = 1.19, P = 0.275 N = 16). On average, 69 successful nests per year were identified (Mean = 68.50, SD = 9.77, N = 6). Because of the challenges of nest detection in this species, the actual total number of breeding pairs is expected to be higher (Walter and Foers 1980). Using the methodology modified from (Dimalexis et al. 2008), we calculated an average of 139 breeding pairs (Mean = 139.40, SD = 8.40, N = 6). Alternatively, based on the nest detection factors proposed by Walter and Foers (1980), the average number of breeding pairs would have been estimated at 124 (Mean = 124.36, SD = 24.56, N = 6). Thirdly, using the intensively studied Akrotiri colony as a proxy for all the other colonies, we estimated that Cyprus hosts 138 breeding pairs (Mean = 137.8, SD = 8.302, N = 6).

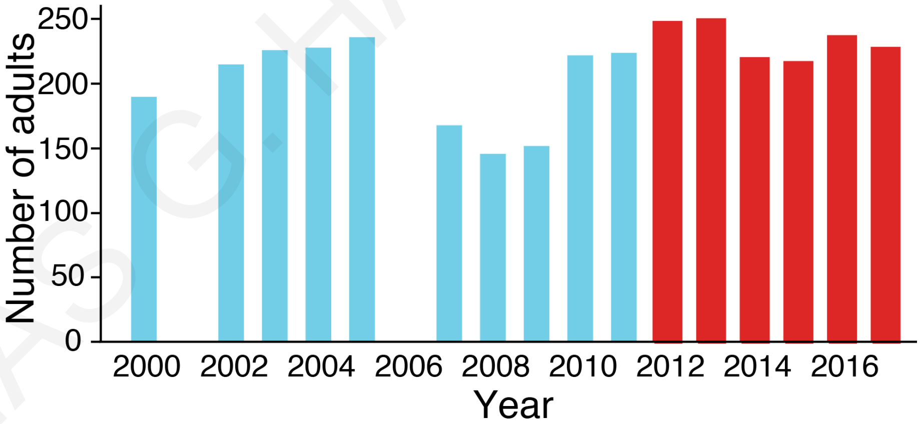

Figure 2: Adults counted during Eleonora’s falcon annual population surveys, in this study (red columns) and based on historical data (blue columns). Previous counts compiled from surveys performed by other groups (Warne 2001; Paton 2003; Pickard and Wilson 2004; Wilson 2005; Miltiadou 2008a; Miltiadou 2008b; Miltiadou 2009; Miltiadou 2011).

Breeding success

A total of 411 successful nesting events were identified during the study period comprising 729 fledglings. The nests at Akrotiri colony spatially reflect the presence of adults observed from the cliff-top surveys early in the breeding season, indicating that adults moving close to the cliff edge can be used to indicate the nesting areas. Nests contained 1 – 3 fledglings (Mean = 1.77, SD = 0.69, N = 411). For Akrotiri colony, these averaged slightly higher (Mean = 1.86, SD = 0.70, N = 168). During the 2013 breeding season, 35 breeding pairs were identified at Akrotiri colony, of which 30 were successful in raising at least one fledgling. Egg stage surveys confirmed that 1 – 3 eggs were laid in each nest (Mean = 2.44, SD = 0.75, N = 27). There were on average 1.90 (SD = 0.86, N = 29) hatchlings per nest, while the average number of fledglings per successful pair was 1.80 (SD = 0.85, N = 30). Overall, we estimated 1.54 (SD = 0.85, N = 35) fledglings per breeding pair (Table 1).

Table 1: Breeding success results of this study, compared with previous work in Cyprus from Akrotiri in 1977 (Walter and Foers 1980) and the Aegean Sea (Xirouchakis et al. 2012)

	Area and period of study				
	Akrotiri	**Akrotiri**	**Cyprus**	**Akrotiri**	**Aegean Sea**
Estimator	**2013**	**2012 - 17**	**2012 - 17**	**1977**	**2004 – 07**
Eggs per nest	2.44				2.43
Eggs hatched per nest	1.90				1.58
Fledglings per successful pair	1.80	1.86	1.77	1.53	1.84 – 2.00
Fledglings per breeding pair	1.54			0.8 – 1.0	1.19-1.75

Nest characteristics

Nests in Cyprus were predominantly located on almost vertical sea cliffs (Mean cliff inclination = 84^o, SD = 11^o, N = 419), at elevations ranging from 1 to 100 m (Mean = 23.71, SD = 20.43, N = 417). Sixty-eight percent of nesting events were on exposed ledges, with 19 % within holes and 8 % in deep ledges (Fig. 3), with a highly significant difference between nest type usage (P < 0.001, N = 419).

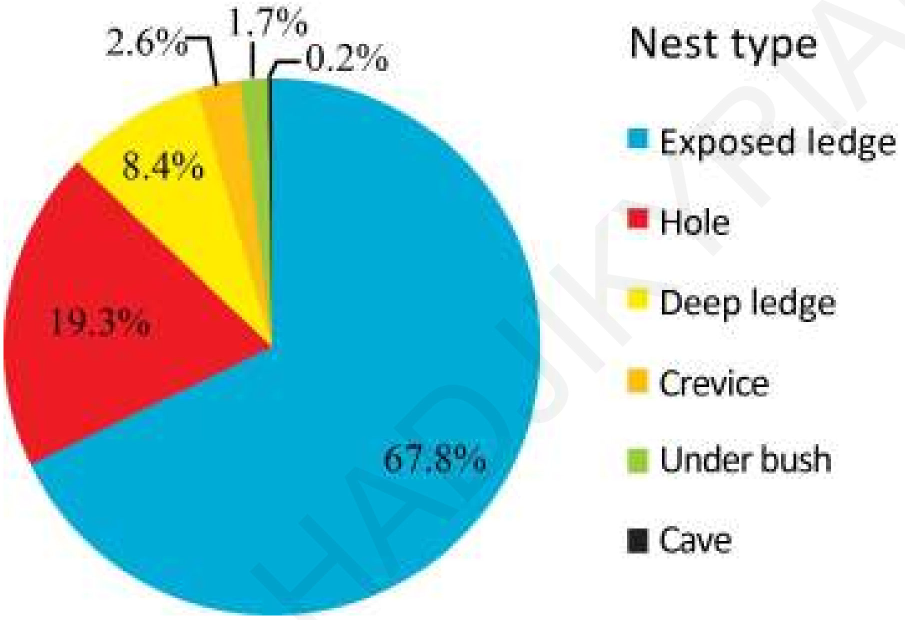

Figure 3: Nest types recorded for Eleonora's falcon in Cyprus for all nesting events from 2012 to 2017 (N = 419).

Nest aspect was predominantly southerly (Mean = 179^o, SD = 40^o, N = 418), with highly significant differences between aspects used (P < 0.001, N = 418). However, for the Akrotiri colony, most nests were also south-facing, but with a slightly more westerly orientation compared to the other two colonies (Mean = 190.40^o, SD = 41.57^o, N = 173). The elevation used at Akrotiri was on average lower than the other two colonies (Mean = 17.14^o, SD = 7.58^o, N = 173) possibly because the cliffs are lower at that colony. DSM for Akrotiri cliffs indicated that out of the potentially available cliff stretch, just a small fraction (1.14 %) is highly suitable for nesting (Fig. 4). This figure is given with the reservation that highly suitable cliff sections with regard to elevation, aspect and inclination, might not provide suitable nesting positions (e.g. ledges, holes and crevices).

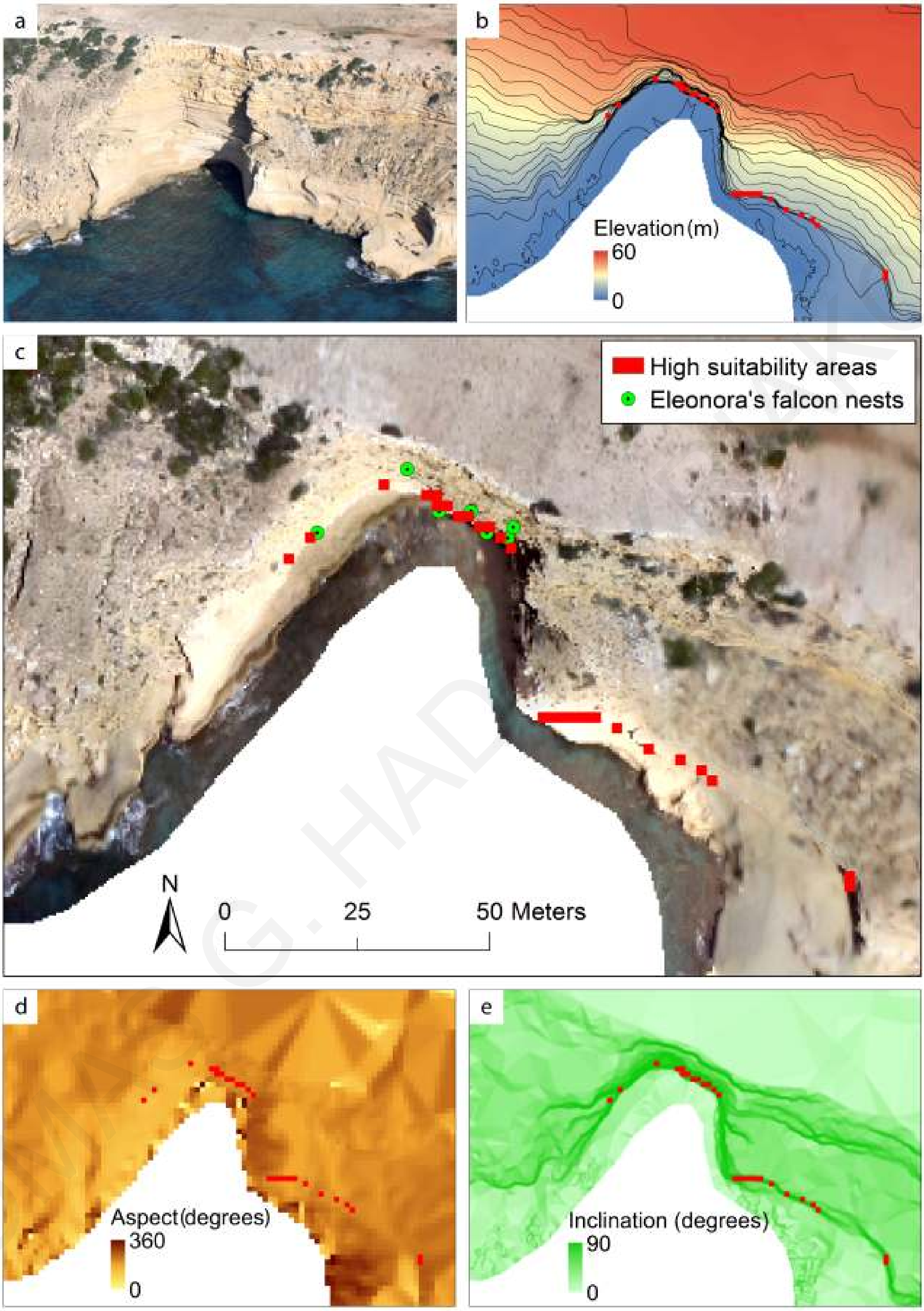

Figure 4: DSM components showing prediction of highly suitable nesting areas at Akrotiri colony, with a) a photo of the cliff section, b) elevation raster, c) orthophotograph of a section of Akrotiri cliffs incorporating actual nests, d) aspect raster and e) inclination raster.

Breeding timings

Based on the observed nestling ages, egg hatching was estimated to have taken place between 15th August and 18th September, peaking on 26th August (Fig. 5). Given that egg laying typically occurs 30 days earlier (Wink et al. 1993; Del Hoyo et al. 1994), predicted peak was on 27th July. Accordingly, fledging normally takes place when nestlings are about 37 days old (Walter 1979; Del Hoyo et al. 1994), therefore, the fledging period is expected to have peaked on 2nd October.

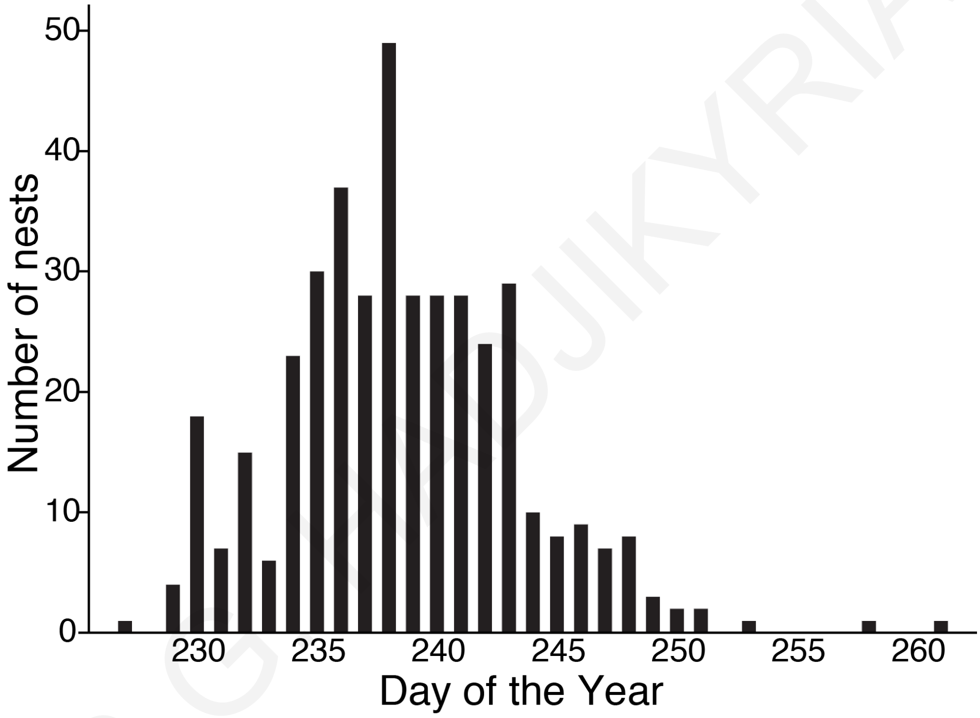

Figure 5: Hatching dates for all nesting events (N = 410) throughout the study period (2012 – 2017) against day of the year.

Effect of nest characteristics and temporal pattern of breeding on breeding success

We found a negative correlation of laying date with breeding success, with early breeders more successful and that precipitation during the pre-breeding season was positively correlated with breeding success (Table 2). For Akrotiri colony during the 2013 breeding season, we found that cliff inclination and nest elevation had a significant effect on the number of eggs laid (Table 2). Hatching success was not affected by any of the variables tested, but fledging success was negatively affected by laying date, with late breeders having significantly fewer fledglings and nest height having a positive effect (Table 2). Nests used repeatedly had a higher number of fledglings ($r_s = 0.346$, $P < 0.01$, N = 63; Fig. 6).

Table 2: Truncated Poisson regression analysis results (non-significant results are not presented) for the factors affecting breeding success stages

Colonies / Years (Stage)	**Estimate**	**Coefficient**	**SE**	**Z**	**P**	**N**
All / 2012 – 2017 (Fledglings)	Laying date	-0.0285	0.0078	-3.66	< 0.001	408
	Rainfall	0.0034	0.0015	2.27	0.024	408
Akrotiri / 2013 (Eggs)	Cliff inclination	0.0346	0.0115	3.00	0.003	27
	Nest elevation	0.0153	0.0061	2.51	0.012	27
Akrotiri / 2013 (Fledglings)	Laying date	-0.0391	0.0162	-2.41	0.016	31
	Nest elevation	0.0214	0.0095	2.25	0.024	31

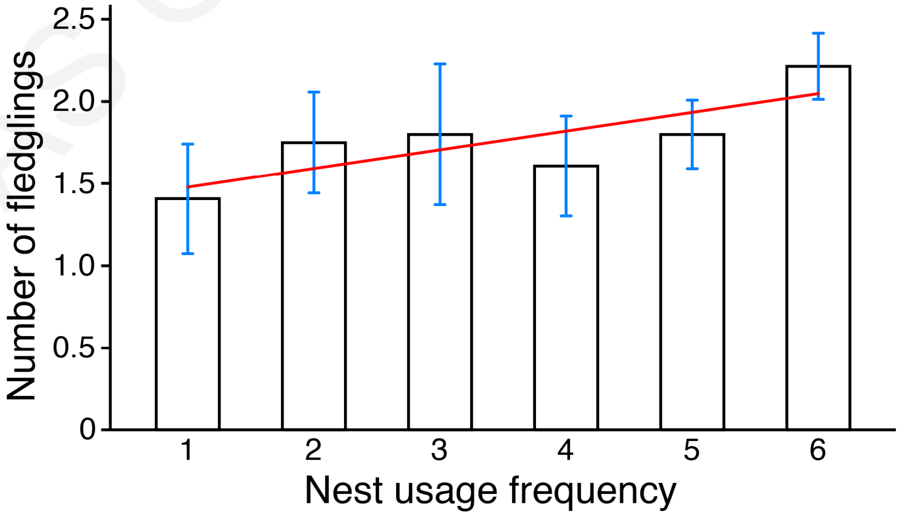

Figure 6: Average number of fledglings over nest usage frequency up to six years, indicates that frequently used nests have a higher fledgling output, as represented by the trendline. Errors bars represent standard error.

DISCUSSION

Long-distance migrating birds are exposed to threats in several parts of their migratory range, thus might be more prone to decline compared to sedentary species (Berthold 2001; Newton 2004; Sanderson et al. 2006). Previous research work on Eleonora's falcon in Cyprus primarily targeted adult population numbers based on counts, the results of which were used to extract conclusions on population trends (Flint and Stewart 1992; Warne 2001). However, considering the strong site tenacity of Eleonora's falcon (Ristow and Bourdakis 1999), its low adult mortality, and its life expectancy (Ristow et al. 1989), which, despite being a long distance migrant (Bildstein 2006) is comparable to sedentary falcons such as common kestrel and peregrine falcon (Cramp et al. 1980; Ristow et al. 1989), a reduction in breeding success can go unnoticed for many years (Ristow et al. 1989). Breeding success largely determines raptor population healthiness, as reductions in breeding success can severely deplete population sizes and lead to local extinction as happened with the peregrine falcon in most of the United Kingdom (Brown 1974). The only previous study assessing comprehensively the breeding success of Eleonora's falcon in Cyprus was conducted in 1977 (Walter and Foers 1980), concluding a surprisingly low level of breeding success, below the sustainability threshold (Ristow and Wink 1985), which raised concerns that this isolated breeding population might be declining (Gschweng et al. 2011), despite the fact that it was considered free of human interference and predation, with nests on isolated steep sea cliffs (Walter 1979; Barov and Derhé 2011).

In this work we used an integrated approach (Newton et al. 2016) to comprehensively assess the breeding success of Eleonora's falcon in Cyprus. This multi-year work reconfirmed population stability (Warne 2001), and resulted in higher than previously suggested estimates for breeding success (Walter and Foers 1980). Indeed, the new estimates are at about the same level as in the Aegean Sea, where the core of the distribution of the species is found (Xirouchakis et al. 2012). Comparing our population results with previous years is not straightforward (Brown 1974), because a different methodology and effort level was practiced between years (Walter 1979; Flint and Stewart 1992; Warne 2001), but we believe the six-year duration of our study, which was conducted with constant effort (same standardised methodology, same observers) and was combined with an intensive breeding success assessment, provides reliable results.

Nevertheless, adult population numbers match historical records in Cyprus from as early as 1972 (Corris 1972), with some variability between years to be expected (Brown 1974).

Although population counts may give an overview of the condition of a colony, they include non-breeding individuals (Dimalexis et al. 2008), including sub-adults, floaters and even non-breeding pairs (Brown 1974; Postupalsky 1974; Steenhof and Newton 2007). Thus, the estimation of breeding pairs needs to be identified instead, because these would be the individuals that actually contribute at any given time to population sustainability, depending of course on breeding success (Brown 1974). In this study, we used three approaches to calculate the number of breeding pairs, based on actual nests identified, but also bearing in mind the adult individuals counted, with the aim of obtaining comparable results with previous studies in Cyprus and elsewhere (Walter 1979; Dimalexis et al. 2008). All three approaches produced similar results, with average estimates between 124 and 139 breeding pairs, thus we can safely conclude that approximately 130 pairs breed in Cyprus.

Different breeding success estimators are often used interchangeably, thus to perform comparisons these need to be clarified (Postupalsky 1974). As a minimum, apart from the number of pairs in a population, the actual breeding pairs need to be identified as well as those successfully rearing at least one fledgling (Brown 1974). We found that in Cyprus the clutch size was at similar levels as in the Aegean Sea (Xirouchakis et al. 2012), which holds at least 80% of the total population of the species (Dimalexis et al. 2008). On the other hand, this is lower than the number of eggs laid at the other extreme of the breeding range in the west (Walter 1979), but this can be attributed to the different food resource bases (Walter 1979). Clutch size has previously been related to male experience and ability to feed the female (Wink et al. 1980). We believe our results support this relationship, based on the positive correlation we found between clutch size and both cliff inclination and nest height and the tendency for more experienced pairs to secure superior nest sites (Ristow et al. 1983). On the other hand, we did not find any effect of laying date on clutch size as in previous studies (Wink et al. 1985). Instead, hatching success was higher in our study compared to findings in the Aegean, where many pairs lay eggs in exposed nests rather than protected sea cliffs (Walter 1979; Wink and Ristow 2000), and rat predation and sun irradiation are evident (Ristow and Wink 1985). The survival between hatching and fledging was affected by the laying date, with early breeders having significantly higher numbers of fledglings per breeding pair, much higher than previous estimates for the same area, i.e. Akrotiri colony (Walter and Foers 1980). Our results ought to alleviate concerns raised by previous studies on the population sustainability (Walter 1979) and possible decline of the Cypriot population (Ristow and Wink 1985; Gschweng et al. 2011) and have since then puzzled researchers. Fledglings per successful pair were also higher than previous estimates and on par with estimates for the Aegean Sea colonies. Because nests in Cyprus are on steep, southerly facing sea cliffs, we did not find any effect of physical nest characteristics on fledglings per successful pair as identified in other areas (Touati et al. 2017). Instead, we found, in agreement with previous studies elsewhere, a significant effect of laying date, with early breeders having higher breeding success (Walter 1979). This indicates that experienced adults, which repeatedly occupy the same superior nests year after year (Clark and Peakall 1977), contribute more to the colony's reproductive success (Perrins 1970), in line with similar findings for Lesser kestrels (Negro and Hiraldo 1993). Precipitation during the pre-breeding season also had a positive contribution to the number of fledglings per successful pair, possibly due to its relation to insect abundance. Clutch size might indeed be affected by insect abundance (Wolda 1978; Wolda 1988), but this becomes more complicated for Eleonora's falcon, because during the nestling raising period it switches its diet to migrant birds, meaning a sufficient pulse of migrant birds is needed to raise offspring (Perrins 1970). Thus, clutch size alone cannot predict higher fledgling numbers, because survival depends on avian prey abundance, given the switch in diet from insects to birds.

We found that the temporal breeding pattern of Eleonora's falcon in Cyprus was almost identical with findings for other colonies, especially in the Aegean (Walter 1968; Walter 1979; Wink and Ristow 2000). We emphasise here the usefulness of indirect calculation of laying, hatching and fledging dates, based on photographic and video evidence of nestlings. The data we obtained from camera traps (Hadjikyriakou and Kirschel 2016) and the intensive work at Akrotiri colony during all breeding stages, allowed us to establish a baseline on breeding stage duration and nestling development stages, and apply it to all the nest and nestling data throughout the duration of the study, involving some 411 successful nests and 729 fledglings. Monitoring the progress of nestling development would not have otherwise been possible, due to either nesting cliff inaccessibility, or lack of resources.

We used data from identified nests to establish a baseline for suitable nest characteristics, which allowed us to predict suitable nesting clusters through the creation of a DSM for Akrotiri cliffs. This combination of photogrammetry techniques with field work can inform the assessment of the carrying capacity of the colony and the potential for colony expansion. Thus, DSM use can aid the prediction of breeding area expansion to other potentially suitable areas, with management objectives aimed at protecting the breeding regions so that population increase can be facilitated (I.A.CO Ltd and BirdLife Cyprus 2016). This work provides the conservation managers of the area with vital information for the protection of Eleonora’s falcon in Cyprus, a designation species of the Special Protection Areas (SPAs) of Akrotiri cliffs, Episkopi cliffs (SBAA 2015) and Cape Aspro – Petra tou Romiou (I.A.CO Ltd and BirdLife Cyprus 2016). The colonies in Cyprus should continue to be monitored, especially in light of new, extensive development projects proposed in the vicinity of the nesting areas (I.A.CO Ltd and BirdLife Cyprus 2016), considerably limiting the major insect feeding grounds identified (T. Hadjikyriakou unpublished data), and the observed increasing recreational activity in the sea off the cliffs (I.A.CO Ltd and BirdLife Cyprus 2016) which has been documented to affect breeding colonies (Martínez-Abraín et al. 2002). In addition, Eleonora’s falcon is quite prone to pesticide poisoning (Xirouchakis 2004), and the suspected increased use of pesticides in crops at major feeding grounds of the species, as well as the use of poisoned baits (I.A.CO Ltd and BirdLife Cyprus 2016) needs further investigation. It is also worrying that bird poaching, including shooting of protected species such as raptors within the wider area around breeding grounds, is one of the highest on the island, including mass persecution of red-footed falcons (Miltiadou 2007). From a total of 340 diurnal raptors found injured or dead in Cyprus (Cyprus Veterinary Services unpubl. records) over the period of the present study (2012 – 2017), 42 % were *Falco* spp., including seven Eleonora’s falcons and authorities need to address these threats. Intraspecific nest predation can be an important factor in breeding success, especially in seasons with limited prey abundance (Gangoso et al. 2015; Hadjikyriakou and Kirschel 2016), thus the monitoring of the migration pulse at Akrotiri can provide valuable information on the sustainability of the colonies in Cyprus, as climate change already affects the phenology of bird migration and insect abundance (Visser and Both 2005).

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CHAPTER 3

Video evidence confirms cannibalism in Eleonora’s Falcon

Video evidence confirms cannibalism in Eleonora's falcon*

ABSTRACT

Cannibalism, though widespread in nature, is considered uncommon in birds. Intraspecific predation has been reported in some species, but evidence is circumstantial, particularly in raptors. Here we describe intraspecific predation in Eleonora's Falcon (*Falco eleonorae*), in a closely monitored colony at Akrotiri Peninsula, Cyprus. By using video cameras, we recorded between-nests intraspecific predation, showing a female feeding her nestlings with a nestling taken alive presumably from a nearby nest. Though such behaviour is rarely witnessed, it could be a common phenomenon whose frequency might be affected by fluctuations in breeding density and food availability.

Keywords: *Falco eleonorae*, camera trap, colonial nesting, Cyprus, intraspecific predation.

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INTRODUCTION

Cannibalism is a widespread phenomenon in the animal kingdom (Polis 1981), but has been thought to occur infrequently in birds (Mock 1984). Such behaviour has been linked primarily with predatory species (Polis 1981), but it has also been observed in non-predatory passerines such as house sparrows (*Passer domesticus*) (Ben-Dov et al. 2006), while in gulls and crows, between-nests predation of conspecific nestlings might be common. In carrion crow (*Corvus corone*) the disappearance of nestlings was attributed to intraspecific nest intrusion and predation (Yom-Tov 1974), while in a large colony of herring gull (*Larus argentatus*) a few cannibals repeatedly fed on conspecific nestlings from within the colony and were also observed feeding their young with conspecific nestlings (Parsons 1971). Several studies on raptors have described within-nest siblicide and infanticide, as well as cannibalism on dead nestling by parents and siblings (Bortolotti et al. 1991; Boal and Bacorn 1994; Sheffield 1994; Margalida et al. 2004; Solaro and Hernán Sarasola 2012), while possible disappearance of nestlings has often been attributed to cannibalism by siblings or parents within the nest (Ingram 1959). Other studies have provided more evidence of cannibalism in raptors. For example, (Jones and Manez 1990) attributed the occurrence of a ring of a conspecific nestling under a black kite (*Milvus migrans*) nest to between-nests predation, but the exact circumstances remained unclear. Arroyo and Garcia (1997) described between-nests cannibalism in montagu's harriers (*Circus pygargus*), but the cause of death could not be determined. Although this behaviour may be less common in falcons which defend their nest, as is the case of American kestrels (*Falco sparverius*) (Bortolotti et al. 1991), cannibalism might be more frequent in colonial nesting birds including falcons due to the higher breeding densities. Negro et al. (1992) made three observations of intraspecific, between-nests predation in lesser kestrels (*Falco naumanni*); (1) an adult unsuccessfully attempted to capture a nestling, (2) an adult successfully captured a nestling and then consumed it, and (3) a conspecific nestling carcass was found in a different nest but there was no information regarding its origin and which individuals, if any, ate it. Breeding density (Polis 1981) and food availability (Gangoso et al. 2015) might play a role in differences in behaviour between falcons, with opportunities to depredate nestlings potentially increasing in colonially nesting species.

Eleonora's falcon (*Falco eleonorae*) is a colonial breeder, nesting on sea cliffs and islets in the Mediterranean and Canary Islands (Walter 1979), and some studies have suggested cannibalism occurs in this species. In 1971, one researcher (D. Ristow pers.

comm.) found a ringed leg of Eleonora's falcon nestling in one nest that had been ringed in another nest 10 m away on the island of Crete, but the circumstances surrounding this event remained unclear. More recently (Steen et al. 2016) recorded an adult Eleonora's falcon stealing a nestling from a conspecific nest using camera traps in Greece in 2014. Furthermore, Gangoso et al. (2015) found 21 rings in several Eleonora's Falcon nests on the Canary Islands, which they attributed to intraspecific predation from nearby nests. In spite of the information so far available, to our knowledge, no study has recorded an Eleonora's falcon performing non-parental infanticide, followed by cannibalistic feeding of the carcass to its nestlings. Herein, we document such behaviour for the first time in Eleonora's falcons. We recorded on video the killing of a conspecific nestling by a female Eleonora's falcon and the subsequent feeding of the nestling to its own offspring.

MATERIAL AND METHODS

We have been studying the breeding population of Eleonora's falcon in Cyprus since 2012, by means of boat, ground and aerial surveys. We estimated the breeding population size on the island at about 130 pairs, including the intensively studied Akrotiri Peninsula colony (hereafter "Akrotiri"), which included approximately 30 breeding pairs. During the 2013 breeding season, we mapped all the nests at Akrotiri; all data were analyzed in ArcGIS 10.1 (ESRI 2012). In addition, during the same breeding season we installed four camera traps in four of the nests to monitor parental care and sibling behaviour. The camera that recorded the cannibalism incident (Table 1) was installed on 23 June 2013 and recovered on 16 November 2013, after both the parents and their fledglings departed to their wintering grounds. Thus, for this particular nest (hereafter, "focal nest"), we obtained video footage covering the entire breeding season. Video activation was triggered by motion, and the system recorded 10 seconds of video footage per trigger activation. The camera was programmed to turn off for a minimum of six minutes before motion could trigger a further recording, thus conserving battery life and memory card space, allowing the covering of the entire breeding period.

Table 1: Camera model, specifications and settings used for Eleonora's falcon nest monitoring in Cyprus

Camera model	**Bushnell Nature View HD**
Sensor	5 MP colour CMOS
Resolution	1920 x 1080 pixels
Night recording	No-glow LED IR flash
Response time	0.7 seconds
Installation date	23/06/2013
Set resolution	640 x 360 pixels
Trigger interval	6 minutes
Recording duration	10 seconds

RESULTS

In the focal nest three eggs were laid, all three of them successfully hatched between 25 and 27 August 2013. On 17 September 2013, when the nestlings were already 21-23 days old, at 11:30 hour, the female parent was in the nest, holding in its talons a live 7-9 days old conspecific nestling, which was fighting to escape (Fig. 1a). By 11:37 hour, the female parent had killed the nestling (Fig. 1b), and started feeding it to its own offspring (Fig. 1c). The incident lasted approximately 30 minutes, with the last relevant recording captured at 11:55 hour (Fig. 1d), during which the dead nestling had been almost completely fed to the nestlings (to see video footage please go to:
https://ucy.ac.cy/biol/documents/Personal/KirschelA/Eleonoras_cannibalism.zip
and download zip file - password: ElefaTHAK).

Figure 1: Frames from the video of the Eleonora’s falcon nest, showing a nestling from another nest brought in alive, then killed by the female parent and fed to the nestlings. a) captured nestling fighting to escape, b) captured nestling just before it was killed, c) dead nestling being fed to focal nest’s nestlings, and d) dead nestling almost completely fed to the nestlings of the focal nest.

During the same morning and prior to the incident there were at least four feeding bouts in the focal nest (07:26 hour, 08:50 hour, 09:13 hour and 11:16 hour), during which the male parent brought food to its mate to feed the nestlings. On those occasions the female was standing over the prey making it impossible to identify. However, we could see that the prey items were small, most likely insects, which might not have been sufficient to satisfy the energy requirements of the nestlings. The cannibalistic event began 14 minutes (11:30 hour) after the last of these four recorded feeding visits. At nine minutes before the incident (11:21 hour), the male parent stood in the nest, while the female was away, presumably capturing the young nestling from a neighbouring nest.

Because the colony was monitored during the entire breeding season we were able to identify the nest from which the nestling was likely taken (hereafter, “target nest”). We did this by identifying those nests that were expected to have nestlings approx. 7 – 9 days old, and then checking if any of them was missing a nestling of that age. We concluded that the target nest was one situated 116 m from the focal nest (Fig. 2): on 19 August, there were three eggs in the target nest. During the next survey on 25 September 2013, there was no sign of any nestlings and the target nest was presumed abandoned.

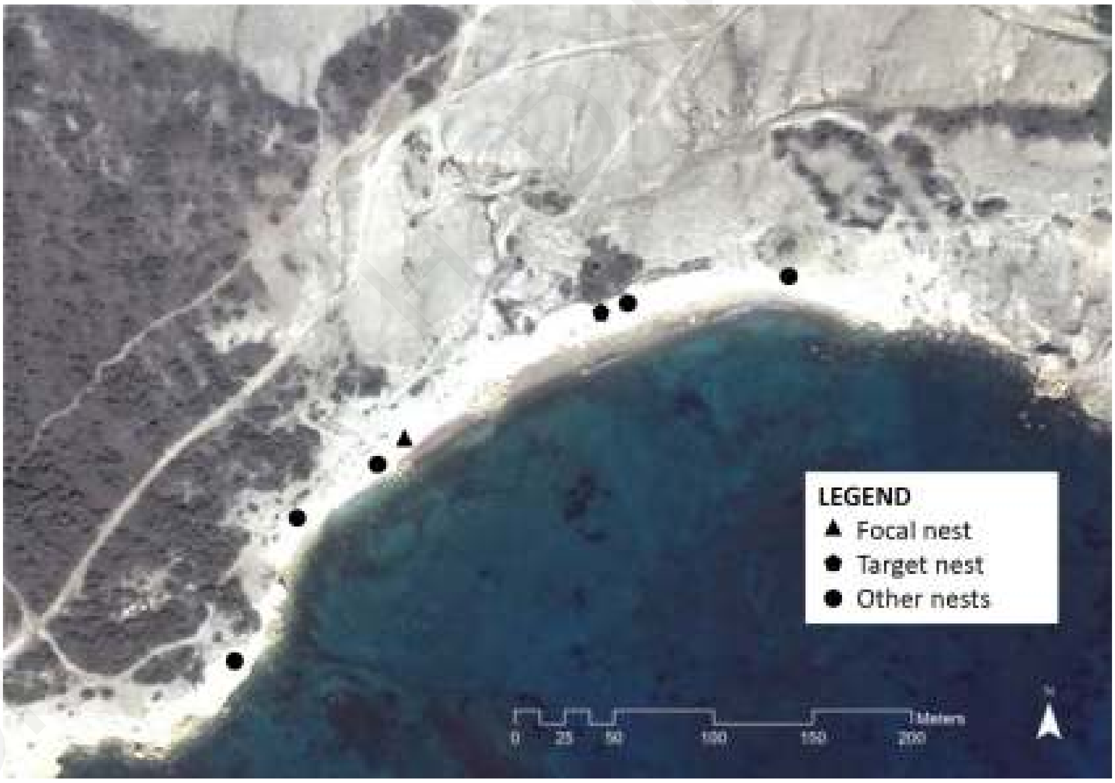

Figure 2: Eleonora’s falcon nesting colony, with focal nest, target nest and other active nests during the 2013 breeding season (background image: ESRI 2012).

DISCUSSION

The focal nest was one of the most successful in our study area on Cyprus over the 3-year study period, with three fledglings each year, which was approximately double the estimated colony mean. Cannibalistic behaviour might have been a contributory factor to the focal pair's high reproductive success. We cannot be certain, however, that the pair occupying the focal nest was made up of the same individuals from year to year, because they were not colour-banded; however, the combination of a dark morph female and a light morph male was consistent over the 3 years. Regardless, the target nest was in direct line of sight of the focal nest, potentially increasing the opportunity for predation by the focal female. We considered predation from the ground (e.g., by rats) unlikely, because the target nest was well protected on a vertical sea cliff. Although other reasons might be responsible for the target nest's reproductive failure, it is possible that the focal pair may also have taken other hatched nestlings from the target nest. We cannot verify this conjecture, because the camera view did not show the entire nesting hole, the female was obscuring the view of some incidents and the camera was triggered at intervals (Table 1) and so did not continuously record activity in the nest.

Because intraspecific predation in birds is rarely witnessed (Jones and Manez 1990), little attention has been paid so far to the role of cannibalistic behaviour in hatchling loss during the breeding season. Among herring gulls, breeding success was substantially reduced by a few persistent cannibals within the breeding colony (Parsons 1971). Indeed, higher breeding density, with more offspring to feed within a colony, may increase the possibility of intraspecific predation (Polis 1981). Likewise, when food is scarce, intraspecific predation may significantly affect breeding success in Eleonora's falcon breeding colonies (Gangoso et al. 2015). Intraspecific predation of nestlings from other nests provides a two-fold benefit from the predator's perspective: food for the predator's young, and fewer nestlings for the colony needing food and thus reduced competition for food resources.

This observation was made possible with the use of camera traps on nest ledges continuously monitoring the nests. Such rare events often go undetected as continuous monitoring of a nest is impractical with traditional manual visual methods (Cox et al. 2012). Thus, modern means of nest monitoring can further contribute to our understanding of breeding ecology and predation behaviour in raptors (e.g. Steen et al. 2016), as well as in birds in general. Further research, including placing more camera traps, with shorter triggering intervals, could help shed more light on the effect of breeding density, food availability and fluctuations in breeding success on the prevalence of such seldom-observed intraspecific predation.

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CHAPTER 4

Habitat influences pathways, travel speed and refueling patterns in migrating falcons

Habitat influences pathways, travel speed and refueling patterns in migrating falcons*

ABSTRACT

Bird migration knowledge at the individual level has significantly improved in recent years due to the use of tracking devices. Until very recently, when satellite tracking studies revealed the routes for a small number of individuals, Eleonora's falcon migratory routes had been effectively unknown. Yet, factors that affect migratory strategy are not well understood, because they require high accuracy, longitudinal data. Here, we use solar-powered GPS transmitters to monitor the migratory movements of Eleonora's falcon breeding in Cyprus, the easternmost breeding population of the species. We tested the relation of speed with vegetative cover, and differences in movements between day and night, comparing also successive trip patterns. We found that tagged individuals repeatedly exhibit an anticlockwise loop migration pattern with spring routes being eastern than autumn. We identified a preference, especially in autumn, for migration through vegetation-rich areas, with lower speeds during daytime, indicating fly-and-forage activity. Birds roosted during most nights, combining refueling stopovers at selected vegetation-rich areas before or after crossing ecological barriers. Conversely, both during day and night, they overflew unsuitable habitats at fast speeds. Our results suggest that habitat is an important factor in Eleonora's falcon migratory strategies, allowing them to combine migration during the day with fly-and-forage refueling, while roosting most nights except when crossing vegetation-poor areas.

Keywords: Route selection, GPS telemetry, remote sensing.

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INTRODUCTION

Migration is part of the annual cycle of many bird species that has evolved over millennia (Alerstam 1993; Sutherland 1998; Newton 2010a). The main driving force is the exploitation of food resource fluctuations at certain times of year (Pulido 2007), avoiding resource depletion especially at breeding grounds (Alerstam et al. 2003). In general, temperature and rainfall fluctuations as well as day length variation within the year establish food availability and determine migratory species presence duration (Newton 2010a). It is believed that current bird migratory patterns have evolved quite recently, within the last 15000 years, during postglacial species range expansions (Sutherland 1998; Berthold 2001; Pulido 2007), resulting in complex systems attracting much research interest (Gwinner and Wiltschko 1978; Alerstam 1993; Nathan 2008; López-López et al. 2010; Newton 2010a Bán et al. 2017). Migration systems are characterised by high precision and accuracy (Thorup and Rabøl 2001; Newton 2010a); indeed they are fine tuned by a number of internal and external factors (Pulido 2007), including genetic instruction, physiological processes, behavioural adaptations to external conditions such as ecological barriers and orientation and navigation mechanisms (Gwinner and Wiltschko 1978; Alerstam 1993; Sutherland 1998; Berthold 2001; Kerlinger 2008; Henshaw et al. 2010). In general, it is accepted that migratory birds have a high spatiotemporal understanding (Nathan et al. 2008), possessing a complex system of compass for orientation, map for navigation, calendar and circannual clock to execute migratory patterns, and sufficient memory to hold this information (Thorup and Rabøl 2001; Newton 2010a). The stronger the endogenous control is on migration, the lower the within-individual variability in migration timing and schedule (Vardanis et al. 2011 López-López et al. 2014), while extrinsic factors such as the effect of weather conditions can have significant contribution as well (López-López et al. 2014). Yet, despite our understanding of the factors that generally dictate migration, less is known regarding how landscape characteristics influence migratory movements (Klaassen et al. 2008), route selection and timing of migration, or the factors which lead to differences between autumn and spring migration, diurnal and nocturnal migrating patterns and stopover choices, as well as fidelity in successive migratory routes (López-López et al. 2014).

Migration strategies of birds are guided by pre-migratory fuel deposition, but refueling en route is equally critical (Alerstam 2011). Bird migration involves cycles of refueling (feeding) en route or at stopovers, and energy spending (moving), until the target area is reached (Åkesson and Hedenström 2007). Habitats frequently used by birds are selected among others (Garshelis 2000), thus, linking movement data with environmental variables is vital to interpreting bird ecology (López-López 2016). Nevertheless, the optimal strategy does not entail stopovers at all potentially fruitful refueling sites, which are instead selected in relation to fuel load, fly-and-forage activity, i.e. hunting while keeping the general direction of travel, and perhaps knowledge of the location of successive stopover sites (Alerstam 2011; Nilsson et al. 2013). Fly-and-forage activity is specifically beneficial to insectivores, which catch and consume prey on the wing, and is believed to be underestimated (Strandberg and Alerstam 2007). Such species must, therefore, select flyways with insect-abundant habitats where they fly at low altitudes to feed while moving (Bildstein 2006). On the contrary, ecological obstacles en route that do not offer feeding opportunities are tackled either by detouring, or by rapid overflying (López-López et al. 2010). Seasonal differences in food availability, but also prevailing wind patterns, are related to acknowledged differences in speed and duration (Berthold 2001; Meyburg et al. 2011; Nilsson et al. 2013), as well as to observed loop patterns between autumn and spring (Alerstam 2011), while overall journey duration may also be influenced by whether or not birds migrate at night. For diurnally feeding species, nocturnal flight is also free of foraging (Alerstam 2009), thus higher overall speeds at night are to be expected (Alerstam 2011). As a strategy, nocturnal continuous flight with foraging during the day may provide the fastest overall migration pace (Alerstam 2009). Raptors, however, are not in general expected to fly at night (Meyburg et al. 2011) unless they are crossing large water bodies (Strandberg et al. 2009a), though finer scale tracking data can tell more about nocturnal flying activity.

Recent technological developments have allowed researchers to gather migration data inconceivable in previous decades (López-López 2016), and field observations have been enhanced gradually by new techniques (Newton 2010a). Ringing has and continues to provide enormous amounts of information (Resano-Mayor et al. 2017; Roth et al. 2017), while radar monitoring has been used to identify migratory movements, especially of bird groups, regardless of altitude and visibility (Alerstam 1993; May et al. 2017). Stable isotopes and genetic markers have also been utilised to provide information on broad scale movements (Arizaga et al. 2016; Schwemmer et al. 2016; Seifert et al. 2016). However, tracking devices of various types attached on individual birds can provide substantial volumes of data throughout migratory trips (Newton 2010a; López-López 2016). Individual tracking devices provide critical information on bird ecology, but as technological constraints limit the use and capabilities of tracking devices (Bouten et al.

2013), researchers prefer to use the most advanced transmitter types available with suitable weight; sample size though is limited in most cases by budget. Today, individual tracking techniques allow for the gathering of extensive amounts of data, revolutionizing animal movement studies (Kerlinger 2008; López-López 2016), and stimulating the emergence of the new discipline of "movement ecology" (Nathan 2008).

Eleonora's falcon (*Falco eleonorae*) is a complete, long-distance, trans-equatorial migrant species (Bildstein 2006; Pulido 2007; Kerlinger 2008), breeding primarily on islands in the Aegean Sea, its presumed original range and centre of its distribution (Walter 1979). The geographic extent of its breeding colonies exhibits an irregular pattern, which relates to the irregular distribution of islands and islets in the Mediterranean Sea. The abundance of preferable habitat within the Aegean Sea, concentrates more than 80 % of its global breeding population within Greece (Dimalexis et al. 2008). The breeding population spreads from Cyprus in the east, westwards along the Mediterranean Sea, the Atlantic coast of Morocco and the Canary Islands (Walter 1979). Almost the entire population overwinters on the island of Madagascar with a small proportion in the Mascarene Islands (Walter 1979) and East Africa (Del Hoyo et al. 1994). The species has evolved to take advantage of unique breeding and wintering niches in the Mediterranean and Madagascar respectively, utilizing abundant resources and avoiding interspecific competition (Walter 1979). Eleonora's falcon feeds predominantly on insects throughout the year, but has a delayed breeding season to coincide with the peak of autumn bird migration passage, with migrants caught on the wing to feed during offspring raising period (Cramp et al. 1980).

In this study, by utilizing GPS accuracy transmitters, we aimed to identify the extent to which Eleonora's falcon migratory routes target favored habitats with rich vegetation, allowing for refueling with fly-and-forage strategy and at selected stopovers. In order to examine specifically whether Eleonora's falcon adapts its strategy with habitat variability, we compared environmental data between recorded points during migration and generated random points. If individuals are moving through the different habitat types without changing their behavior, especially speed, this would mean there is no preference. On the other hand, adaptation of speed in relation to habitat characteristics would indicate that the presence in specific habitats could be linked to specific activity, such as fly-and forage. Furthermore, we compared and contrasted migratory strategy between seasons, determining the speed travelled over different habitats during day and night. We expected individuals to fly faster over habitats unsuitable for foraging, such as extensive water bodies and deserts. In addition, the duration of the study provided the opportunity to have an overview of the spatial and temporal route fidelity of consecutive trips, which can provide useful conservation guidance (García-Ripollés et al. 2010), especially if fidelity is high (Shiu et al. 2006).

MATERIAL AND METHODS

Field methods

Cyprus hosts around 130 pairs of Eleonora's falcon nesting at the south coast of the island, from Cape Gata at Akrotiri Peninsula in the east, to Cape Aspro in the west. Between 2013 and 2017 we monitored the year-round movements of Eleonora's falcons originating from Cyprus using for the first time GPS telemetry technology providing high spatial and temporal detail. In particular, we attached twelve transmitters on individuals breeding at Akrotiri colony in Cyprus, of which eight provided us with useful migration related data (five female adults, two male adults and one juvenile) (Table 1).

Table 1: Details of individuals, tag types, recorded trips and filtered locations

Tag type	**Name of individual**	**Sex**	**Age**	**Date of capture**	**Autumn trips**	**Spring trips**	**Number of locations**
GPS	Eleni	Female	4th year+	2/6/13	2	2	131
GPS	Ifigeneia	Female	3rd year	7/6/13	1		334
GPS	Farofylakas	Female	4th year+	10/9/13	4	3	658
GPS	Mitsis	N/A	1st year	17/10/13	1		254
GPS	Pappous	Male	5th year+	17/6/14	1		40
GPS	Forsman	Male	4th year+	17/10/14	1		161
PTT	Aneti	Female	4th year+	30/9/13	1		94
PTT	Tsampoukalou	Female	4th year+	30/9/13	1		44
				TOTAL	**12**	**5**	**1716**

Birds were caught using mist nets at nest and forage locations (Bildstein and Bird 2007). To this end, a mist net was placed on a cliff top opposite nests at the southern edge of the Akrotiri peninsula. A taxidermic mount of eagle owl (*Bubo bubo*) was used as a decoy to attract falcons with luring (Limiñana et al. 2012). In addition, four nets were set within an olive grove, where the falcons had been observed feeding on large beetles at dusk. Birds were handled in accordance with standard procedures (Gosler 2004) and marked with metal rings (Redfern and Clark 2001), while biometric measurements including body mass were taken (Dawson 2004). Transmitters were attached with a teflon harness as a backpack (Kenward 2000). Two different types of solar transmitters were used: ten GPS-GSM loggers from Ecotone Telemetry, and two Platform Transmitter Terminals (PTTs) from Microwave Telemetry. The weight of the transmitter ranged between 1.5 % and 5 % of the bird's mass. No abnormal behavior was observed after transmitter attachment (Barron et al. 2010), with individuals moving as expected between breeding and foraging areas over subsequent days. GPS-GSM loggers sent locations through the GSM network on a user defined temporal pattern, while PTT transmitters were set on a pre-programmed standard duty cycle of 10 hours on followed by 48 hours off (Microwave Telemetry 2013).

Data filtering

Positional error of GPS-GSM locations was less than 20 m for 80 % of the retrieved points (Ecotone 2013), thus we retained all available points for further analyses (but see autocorrelation related filtering below). The Kalman filtering algorithm was used to enhance the varying accuracy of PTT positions, which is divided in seven location classes (i.e., LC3 < 250 m, LC2 250 - 500 m, LC1 500 - 1500 m, LC0 > 1500 m, LCA and LCB = Unbounded accuracy, LCZ = Invalid location) (CLS 2013). Although LC3, 2 and 1 are typically considered as high quality (accuracy) locations (Thorup et al. 2003), Hays et al. (2001) showed that LCA had similar accuracy with LC1, while LC0 were far less accurate than LCA. Thus, in cases where we had to choose between which points to exclude (see subsequent filtering) we used the following order of priority: B, 0, A, 1, 2, 3. Consequently, points of all location classes apart from LCZ were used as long as they followed the general travel direction, assessed through visual inspection of the points in Google Earth (Hays et al. 2001; Limiñana et al. 2012; López-López et al. 2014; Vardanis et al. 2016). For the analyses we excluded locations, either GPS or PTT, less than an hour apart to avoid spatial autocorrelation (Otis and White 1999; López-López et al. 2010; Limiñana et al. 2012; López-López 2016). Likewise, for PTT locations we additionally excluded those lying less than a kilometer apart (Otis and White 1999; López-López et al. 2010; Limiñana et al. 2012; López-López 2016; Kassara et al. 2017).

Estimation of path metrics

Distance and speed between consecutive locations was calculated in ArcGIS 10.1 based on the geodesic distance (Jorge et al. 2011), i.e. the shortest line between any two points on the earth's surface considering the curvature of the earth (ESRI 2012). Estimated speed is compromised if location accuracy is poor (i.e. PTT obtained locations) combined with short distance between points (Hays et al. 2001), because such a sequence of points could also represent a static bird inconsistently localized on successive fixes. On the other hand, the longer the time between two consecutive points, the more likely that the speed will be biased towards the overall movement pace rather than approaching the actual flight speed, as in-between movements, e.g. foraging activity, are increasingly overlooked (Desholm 2003). Consequently, we decided to rely only on GPS positions for speed estimates. In order to assign a position to day or night, sunset and sunrise information was obtained for each position based on local times (Morrissay 2017), with half an hour before sunrise and after sunset included as daytime, to reflect the crepuscular ecology of the species (Walter 1979). To identify active migratory movements, we used only path segments where the speed was > 5 km/h (Strandberg et al. 2009a; López-López et al. 2010; Mellone et al. 2013). To assess consecutive trips spatial fidelity, tracking points were converted to lines (Fig. 2), and after visual inspection, maximum distance in-between each pair of lines was measured manually using the geodesic distance in ArcGIS 10.1 (ESRI 2012).

Habitat use at stopovers and roosts

As stopovers we considered areas with a 25 km radius where an individual stayed for at least 24 hours without exhibiting directional migratory movement, allowing one outlier point per stopover (Limiñana et al. 2012; van Wijk et al. 2012). Habitat use during night roosts, based on consecutive positions indicating that individuals were stationary, was identified by overlaying obtained migration positions onto a MODIS land cover layer (NASA 2018). Two resolutions of land cover were used; a finer available one with a resolution of 500 X 500 m (MCD12Q1) to reflect high GPS accuracy locations and a coarser one with about 5 X 5 km resolution (MCD12C1) to match the lower accuracy of PTT transmitters. To further utilize the high spatial accuracy of the GPS locations, Google Earth (Google Inc. 2013) was used to identify habitat details at roost and stopover areas such as single trees within croplands, which could not be identified within remotely sensed habitat datasets (Klaassen et al. 2010).

Route selection in relation to habitat characteristics

In order to determine whether Eleonora's falcon chose to migrate over areas with specific vegetative cover requirements, we compared actual bird positions with random locations generated within a 50 km buffer, either side, of each trip (Sutherland et al. 2004); this distance is expected to be well within the range of vision of the tracked individuals (Alerstam et al. 2006). If individuals do not actively utilize vegetation-rich areas, they would appear to fly at a similar pace throughout their migratory journey, with roosts and stopovers located over any habitat type encompassed along the route. Thus, for each trip we generated 150 random points in Geospatial Modelling Environment (GME) 7.2.1 (Beyer 2014), to provide a total number similar to the total number of recorded positions for use in statistical analyses. We used the Normalized Difference Vegetation Index (NDVI) obtained from the Moderate-resolution Imaging Spectroradiometer (MODIS) sensor on the Terra satellite (NASA 2018), as a proxy for the greenness along the migratory routes (Klaassen et al. 2010), and as an indication of food availability for the migrating falcons (Mellone et al. 2013; Trierweiler et al. 2013). Sixteen-day NDVI granules (nominal resolution 250 X 250 m) were downloaded covering the extent of migration period, and the granule that overlapped most with the duration of each trip event was used to extract the relationships separately. Data (actual and random) were also overlaid over a percent tree cover layer (hereafter ‘tree cover’) i.e. the vegetation continuous field product (nominal resolution 250 X 250 m) also from the MODIS sensor (NASA 2018). Elevation data were extracted from the United States Geological Survey website and had a resolution of 7.5 arc-sec, i.e. about 150 X 150 m (USGS 2016). All environment data were extracted using ArcGIS 10.1 (ESRI 2012). For GPS positions the nominal NDVI, tree cover and elevation resolution was used, but for PTT positions with lower accuracy, bilinear interpolated data, which incorporate adjacent cell values in the value calculation, were extracted. For habitat selection analyses we excluded actual locations and random points over the sea and other extensive water bodies where EVI and tree cover were not available. We investigated which environmental characteristics affect route selection of Eleonora’s falcon during migration for each season, with the use of Generalized Linear Mixed Models (GLMM) with a binomial distribution and logit link function in lmer in R 3.4.3 (R Core Team 2018). Specifically, we tested for the effects of NDVI, tree cover and elevation as fixed variables with individual and year as crossed random factors and a binary value for whether a point represented an actual position or a random point as a dependent variable. We used Akaike’s Information Criterion (AIC) to select the best model for each test.

Speed differences in relation to season, habitat characteristics and daily activity

Because travel speed is related to the activity of the tracked individuals, for example slower speeds are expected when birds are foraging, we investigated which factors affect the travel speed of Eleonora’s falcon during migration with the use of Generalized Linear Mixed Models (GLMM) with a Gaussian distribution with identity link function using lme4 in R 3.4.3 (R Core Team 2018). Specifically, we tested for the effects on travel speed of NDVI, percent tree cover, elevation and season, as well as the interactions between the environmental variables and season, with individual and year as crossed random factors. Because of the high number of trip segments recorded as transitioning between day and night, we additionally ran separate models without these transitioning segments to investigate how NDVI, tree cover, elevation and season affect travel speed during the day and at night, including their interactions with day and night, again with individual and year as crossed random factors. We ran a separate model including all recorded flights, and another including only flights over 5 km/h to focus specifically on active migratory speeds. We again used AIC to select the best model for each test.

RESULTS

Description of migratory routes

From the eight Eleonora's falcons tagged that provided migration related positions (Table 1), we obtained data for seven migration seasons (four in autumn and three in spring) between 2013 and 2016, on a total of 17 individual migratory events (12 autumn and five spring). Following data filtering of low quality positions, and eliminating potential sources of autocorrelation, we retained 1716 positions (1578 GPS and 138 PTT). Autumn migration duration was on average longer (N = 8, mean = 24.75 days, SD = 11.52) than spring migration (N = 3, mean = 19.33 days, SD = 4.16), though we note that the confirmed durations in spring come from only one individual (Farofylakas) for which the comparative results indicate the same average duration (Autumn: N = 4, mean = 19.00, SD = 10.03; spring: N = 3, mean = 19.33, SD = 4.16). In autumn, departure from Cyprus occurred between 4th October and 6th November, with the peak around 26th October (8 out of 12 confirmed departure dates falling between 24th and 27th October). Arrival in Madagascar occurred between 8 and 28th November without any obvious peak. In spring, departure from Madagascar was between 9 and 15th April, and arrival in Cyprus between 25th April and 9th May (Fig. 1).

In autumn, tagged falcons appeared to fly non-stop south upon initiating migration. They crossed the Mediterranean from Cyprus, and once across, most routes were over the Sinai Peninsula, along the western coast of the Red Sea and over the Sahara Desert at its narrowest crossing in the East. After crossing the Sahara, individuals roosted for most nights from there onwards, including one or two stopovers for most routes within savannah in Ethiopia, Sudan or Kenya. Routes continued southwards towards Mozambique, from where on occasion individuals headed eastward for refuelling stopovers prior to the crossing of the Mozambique Channel to Madagascar (Fig. 2a). In spring, the tagged falcons crossed the Mozambique Channel, often straight over Zanzibar to Tanzania. They then moved through eastern Kenya to Ethiopia and Somalia, where they had a short stopover before following a more easterly route than in autumn, primarily along the east coast of the Red Sea, east of the Sinai Peninsula, and then across the Mediterranean to the breeding grounds in Cyprus (Fig. 2b). The speed over latitude relationship shows that there were sites at specific latitudes with concentrations of stopovers for roosting and foraging. The autumn concentration of points around 10 – 13° N, suggests that there was a major stopover upon reaching savannah after rapidly overflying the Sahara desert. Then, after this refuelling stop, there were further autumn concentrations representing stopovers, especially around - 2° S and -15° to -17° S. The main apparent stopover in spring occurred around 8° to 9° N. In addition, very few night roosts were observed from 13° to 32° N, indicating continuous flight day and night (Fig. 4b). In autumn, tagged individuals roosted predominantly in savannah (62% of nights spent roosting), while in spring they roosted mostly in shrubland (65%) (Fig. 3).

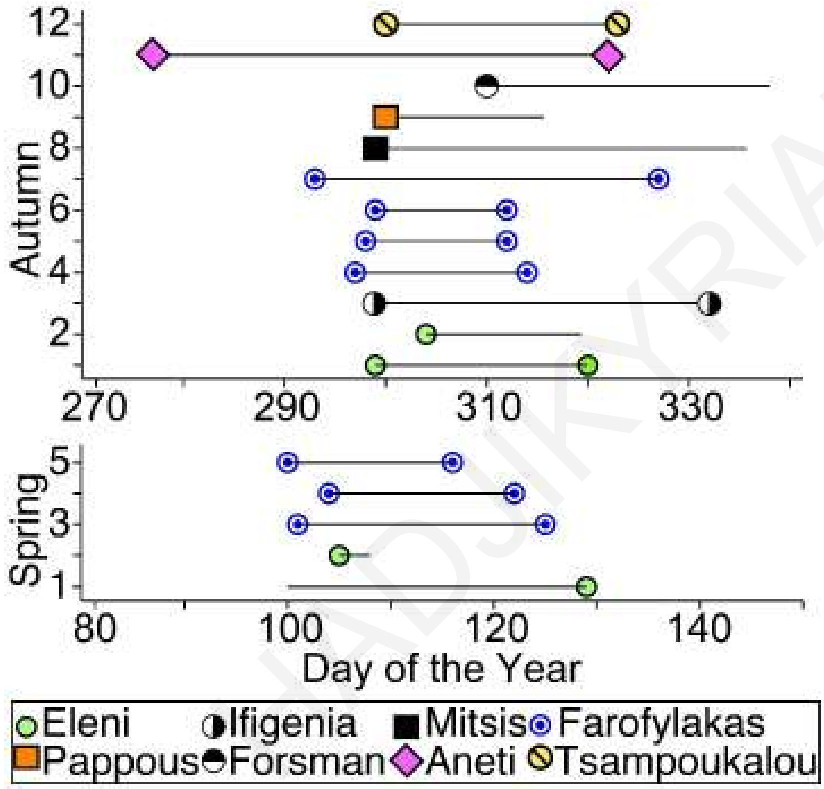

Figure 1: Recorded departure and arrival dates for Eleonora's falcon migration events in autumn and spring. Lines indicate duration between departure and arrival (Madagascar and Cyprus) while symbols represent exact departure and arrival dates for each trip where known (each individual is represented with different symbol as shown in the legend, with consecutive trips for repeatedly tracked individuals bunched together). To aid comparison, day of the year was used.

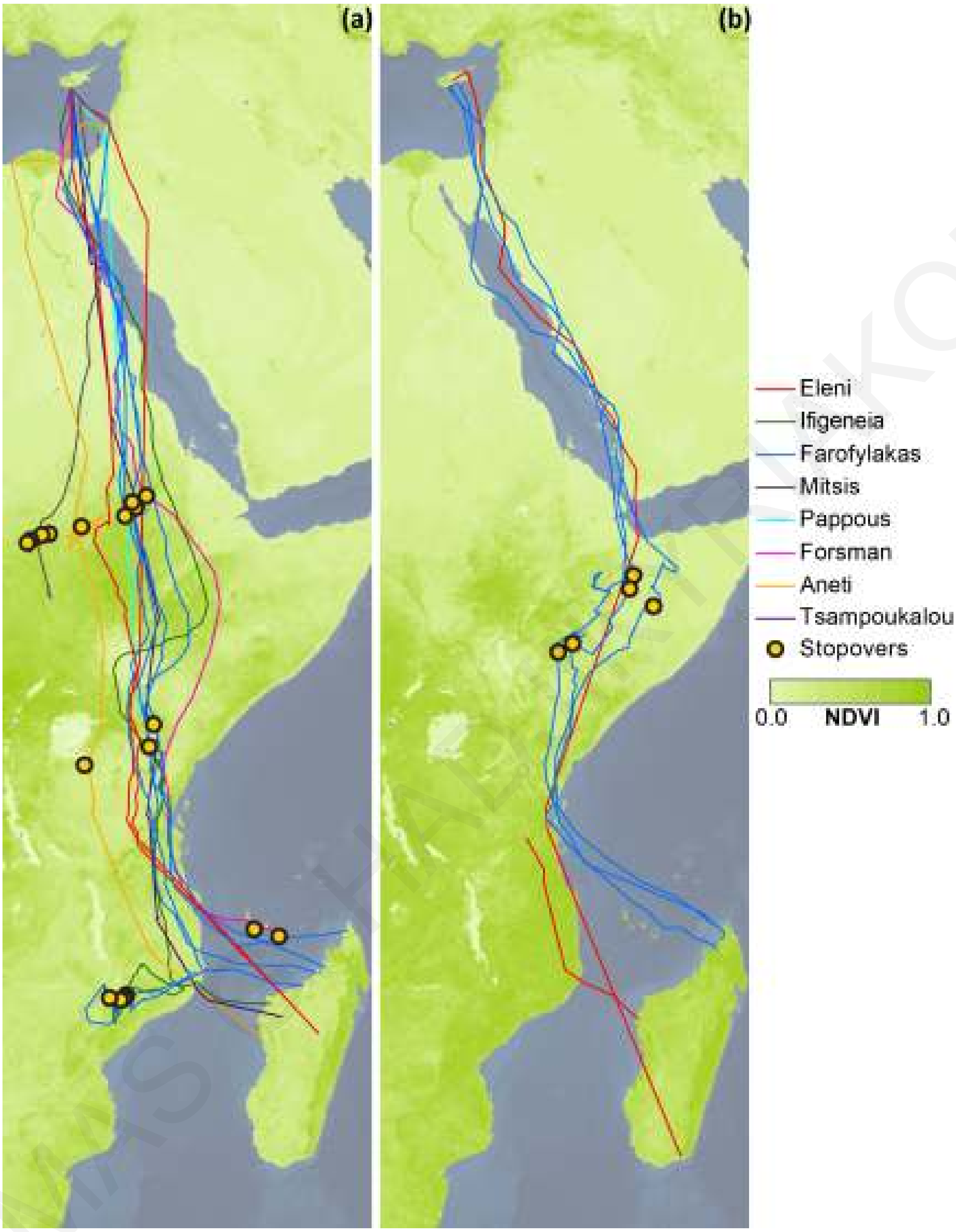

Figure 2: Migratory routes during (a) autumn and (b) spring overlaid on to the respective NDVI raster data for each season. Line colors represent the different individuals. Yellow points denote stopovers. Autumn routes are further west than spring ones resulting in a loop migration pattern.

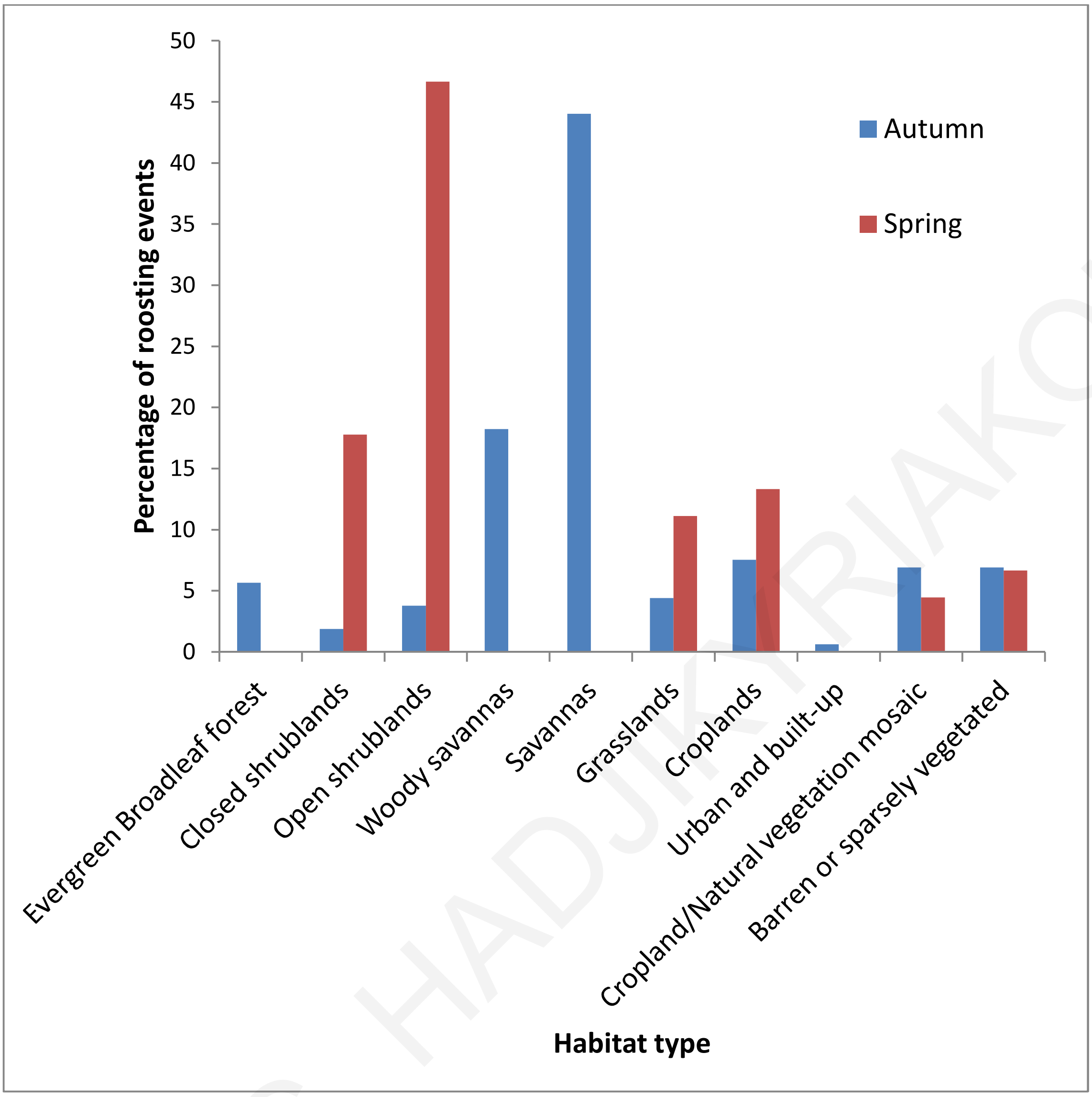

Figure 3: Roosting habitat types in (a) autumn and (b) spring. The majority of roosts in autumn were in savannah (62 %), while in spring they were in shrublands (65 %).

Route selection and movement pace in relation to habitat characteristics

The average distance covered in autumn was 7139 km (SD = 1320), compared to 7245 km (SD = 401) in spring. The shortest path distance for each trip was 5749 km (SD = 209) in autumn and 5845 (SD = 626) in spring, so actual distances traveled were about 24 % further than the minimum possible distance. The longest apparently continuous flight, recorded for Ifigeneia, was 3530 km, covered in 85 hours with an average speed of 40 km/h (maximum single segment 73 km/h). The two individuals that provided us with migratory data from multiple years indicate temporal (Fig. 1) and spatial fidelity (Fig. 2). Specifically we found that four complete autumn consecutive trips of the same individual were situated in a corridor with a maximum longitudinal width of less than 300 km. Furthermore sections of about 4000 km and 1000 km in consecutive trips of the same individual were lying in corridors with a maximum width of less than 100 km and 10 km respectively. With regards to temporal fidelity, we found that three consecutive trips of the same individual were not differentiated between them throughout the whole duration of autumn migration for more than 48 hours at any latitude. In both seasons, the falcons used areas with higher NDVI compared to generated random points (Table 2). They also occupied area with higher tree cover and lower elevation than random points within the 50 km buffer zone either side of their path in autumn, but not in spring (Table 2).

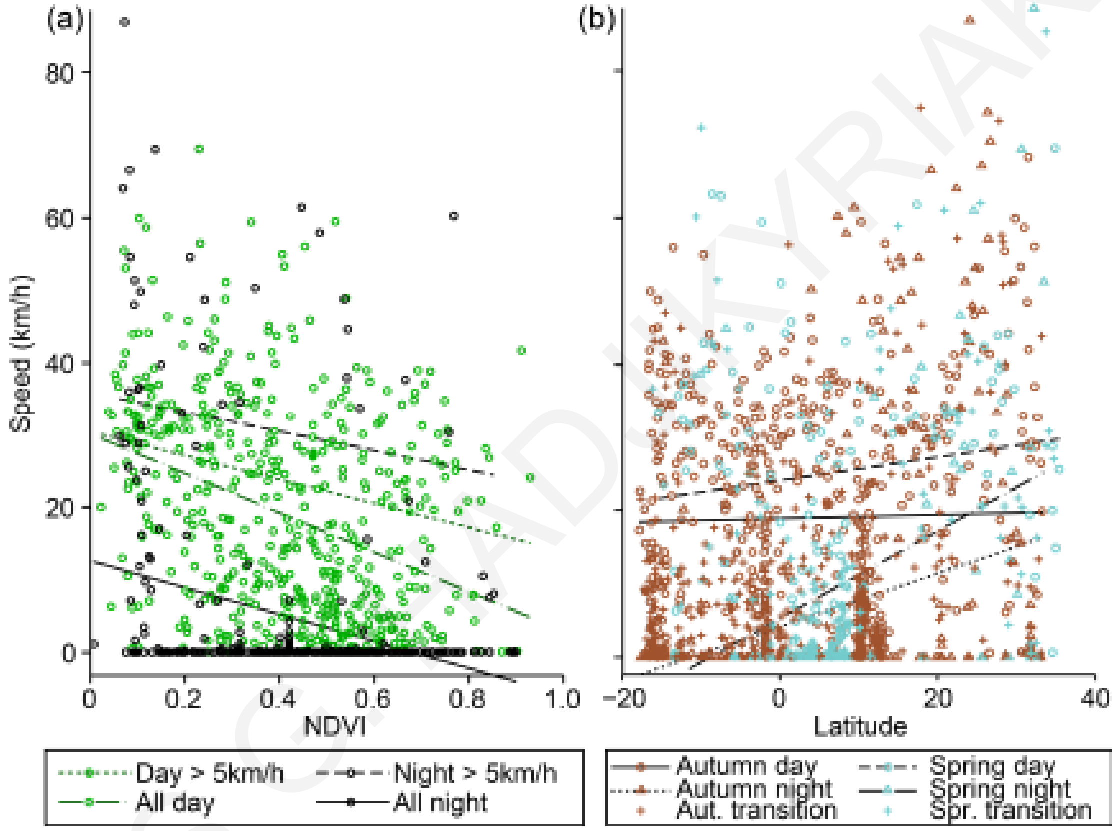

Figure 4: (a) Flight speeds over NDVI with lines of best fit, during day and night, for all time periods between GPS positions, and for those described as active migration (speeds > 5 km/h), but excluding transitions between day and night. Speeds were significantly lower over areas with higher NDVI, with slower speeds overall recorded at night suggesting birds roost during most nights. By including only presumed active migratory movements (speeds > 5 km/h), speeds were typically higher at night than during the day. (b) Speed over latitude for autumn and spring, including night, day and transition flights between day and night. There are sites at specific latitudes with concentrations of points, which indicate stopovers for roosting and foraging.

Table 2: GLMM results for comparison between actual and random points within a 50 km buffer zone either side of their path, in relation to NDVI, tree cover and elevation for a) autumn and b) spring seasons

a)		**Autumn (N = 2873)**			
Variable	**Estimate**	**SE**	**Z**	**P**	**AIC**
NDVI	0.0002	0.00003	8.41	< 0.001	3466.70
Tree cover	0.0107	0.0041	2.64	0.008	3466.70
Elevation	-0.0002	0.0001	-2.38	0.017	3466.70
b)		**Spring (N = 857)**			
NDVI	0.0002	0.00004	3,92	< 0.001	918.10
Tree cover	-0.0241	0.0197	-1.22	0.221	918.55
Elevation	0.0004	0.0002	1.90	0.058	918.10

Birds mostly roosted at night, with the average diurnal and nocturnal movement pace of 20.02 km/h (N = 588, SD = 15.33) and 6.41 km/h (N = 474, SD = 15.94) respectively. However, when considering only active migratory movements, travel speed was on average faster at night with 35.61 km/h (N = 84, SD = 19.98) compared with the day with 25.42 km/h (N = 454, SD = 13.25) (Fig. 4a). The highest travel speeds were recorded at night, both in autumn and spring, over the Mediterranean, Sinai and the Red Sea with a maximum speed of 89 km/h. Speeds were significantly lower over areas with higher NDVI and higher tree cover, with differences in speed in different elevations being higher in autumn than in spring (Table 3). After excluding the transitioning segments between day and night, slower speeds were recorded at night and again over higher NDVI in this dataset (Fig. 4a and Table 4), with differences in speed between day and night being greater in autumn than in spring (Table 4). Conversely, by including only presumed active migratory movements (speeds > 5 km/h), we found that speeds were still slower over higher NDVI, but higher during the night compared to day (Fig. 4a and Table 5). The effect of increasing tree cover percentage on speed was higher during the day compared to night (Table 5). Also, the difference in speed between day and night was again higher in autumn compared to spring (Table 5).

Table 3: GLMM results for the effect on speed, of NDVI, tree cover, elevation, and season, with interactions of season with the other fixed effects

Effect		Estimate	SE	t	P	AIC
Fixed effects	NDVI	-0.0022	0.0002	-9.306	< 0.0001	11565.00
	Tree cover	-0.0683	0.0317	-2.157	0.0310	11565.02
	Elevation	0.0009	0.0007	1.266	0.2056	11566.06
	Season	0.0624	2.3900	0.026	0.9792	11580.02
Interactions	NDVI: season	0.0001	0.0006	0.139	0.8894	11580.02
	Tree: season	0.2012	0.1477	1.362	0.1732	11580.02
	Elevation: season	-0.0073	0.0002	-3.422	0.0006	11580.02

Table 4: GLMM results for the effect on speed of NDVI, tree cover, elevation, season and day/night (excluding transitioning segments between day and night) with the interactions of day/night with the other fixed effects

Effect		Estimate	SE	t	P	AICc
Fixed effects	NDVI	-0.0023	0.0002	-11.102	< 0.0001	7798.85
	Tree cover	-0.0416	0.0502	-0.827	0.4081	7819.72
	Elevation	0.0000	0.0010	0.012	0.9903	7846.97
	Season	-0.7223	1.7010	-0.425	0.6712	7798.85
	Day/night	-12.8400	0.8750	-14.669	< 0.0001	7798.85
Interactions	NDVI: day/night	0.0008	0.0005	1.749	0.0803	7819.72
	Tree: day/night	-0.0704	0.0685	-1.027	0.3045	7819.72
	Elevation: day/night	-0.0008	0.0015	-0.555	0.5790	7846.97
	Season: day/night	-5.6240	2.2950	-2.450	0.0143	7798.85

Table 5: GLMM results for the effect on active migratory movements' speed of NDVI, tree cover, elevation, season and day/night, with interactions of day/night with the other fixed effects

Effect		Estimate	SE	t	P	AICc
Fixed effects	NDVI	-0.0017	0.0003	-5.759	< 0.0001	3698.68
	Tree cover	-0.0653	0.0627	-1.042	0.2976	3700.82
	Elevation	0.0001	0.0011	0.101	0.9197	3736.57
	Season	0.2430	1.8830	0.129	0.8972	3698.68
	Day/night	9.5960	2.0300	4.726	< 0.0001	3698.68
Interactions	NDVI: day/night	0.0017	0.0010	1.681	0.0928	3712.00
	Tree: day/night	-0.2613	0.1219	-2.143	0.0321	3700.82
	Elevation: day/night	0.0031	0.0033	0.951	0.3414	3736.57
	Season: day/night	-15.5600	4.4280	-3.515	0.0004	3698.68

DISCUSSION

Eleonora's falcon breeding in Cyprus flew due south towards their wintering grounds in Madagascar, but in spring they returned via a more eastern route, resulting in a loop pattern in accordance with findings in previous studies, but further east of those, reflecting the geographical relationship between breeding and wintering grounds (Kassara et al. 2012; Mellone et al. 2013). Both average distances covered and migration duration were found to be similar between seasons, in contrast with findings for birds tagged in western Mediterranean (Mellone et al. 2013), but with the caveat that complete spring route data from our study involved a single individual (Farofylakas). Departure dates from breeding grounds formed a very narrow window, peaking on 26th October, in agreement with previous results from other colonies (Gschweng et al. 2008; López-López et al. 2010; Kassara et al. 2012), while in spring the narrow migration window we found coincides with that found for birds breeding in the western Mediterranean (Mellone et al. 2013). Our data from GPS transmitters confirm that returning birds go to their breeding colony at the end of their spring migration, before dispersing again for pre-migratory ranging (T. Hadjikyriakou unpubl. data).

We believe that the consistency in times of departure and arrival, the relatively small latitudinal temporal differences between consecutive trips and the short distances between consecutive routes, are indicative of spatial and temporal within individual fidelity, in the manner of 'calendar birds' (Berthold 2001). This contradicts results for birds tagged in the Eastern Mediterranean for which no within individual fidelity was identified, with longitudinal distances between consecutive trips found to be up to 1200 km in autumn and 2800 km in spring (Gschweng et al. 2008; Mellone et al. 2013). Eleonora's falcon overwinters in a relatively small area, primarily on Madagascar, indicating that the species is using external navigation cues (Gschweng et al. 2008) in addition to internal mechanisms of orientation (López-López et al. 2010). Considering the presumed within-individual high fidelity versus the between-individual relatively higher spread, we suggest that Eleonora's falcon follow a genetically imprinted route (Berthold 2001; Kerlinger 2008; Nathan et al. 2008) towards the wintering grounds. As soon as they establish an optimal route and survive, they remember and copy it for consecutive years (Berthold 2001), enhancing migration success (Bildstein 2006).

The preference of the tracked individuals for vegetation-rich areas and the observed slower speeds over those areas, especially in autumn, indicate that birds spend time refuelling in those more richly vegetated areas, possibly with fly-and-forage strategy, thus reducing the necessity for regular stopovers (Klaassen et al. 2008). In addition, because of the high spatial accuracy and more consistent temporal position collection of this study (with the use of GPS transmitters), we were able to show that, in contrast to findings for birds breeding in eastern Mediterranean, birds roost during most nights in vegetation-rich areas, primarily in savannah in autumn and shrublands in spring, (López-López et al. 2010), resulting in significantly slower migration movement pace at night. This further supports the fly-and-forage assumption, as although migration movement pace was higher during the day (attributed to night roosts), when considering only active migratory movements (speed > 5 km/h) even over more richly vegetated areas, speeds were significantly faster at night, when the birds would not be foraging when flying. Over vegetation-poor areas though, they appear to fly day and night with even higher average speeds at night compared to day, as they fly solely for migratory purposes, and possibly in better flying conditions (Alerstam 2009). This is in line with recent findings that upon facing the challenge of crossing an ecological barrier, birds are able to adapt their diurnal and nocturnal flight patterns to overcome it as quickly as possible (Adamík et al. 2016). This is in accordance with expectations (Alerstam 2009) and supports the hypothesis that vegetation-poor areas are ecological barriers for Eleonora’s falcon (López-López et al. 2010), which they overcome by rapidly traversing rather than seeking a detour (López-López et al. 2010; Kassara et al. 2012; Mellone et al. 2013), with higher speeds over sea and desert (Tottrup et al. 2012). This indicates that landscape characteristics are guiding the routes and the movement pace (Klaassen et al. 2008), with individuals behaving as ‘sprinting migrants’ when feeding opportunities are lacking such as over the Sahara desert (Klaassen et al. 2008). In autumn the Sahel, south of the Sahara, is quite green with an abundance of flood pools and insects (Newton 2010a), so birds benefit from refuelling after the Sahara crossing, but in spring the Sahel is at its driest, with potentially less food available (Newton 2010a), possibly contributing to the observed loop pattern. The short rainy season in eastern Ethiopia in spring might facilitate movements through there because of a timely abundance of potential insect prey (Newton 2010a), as suggested similarly for red-backed shrikes (Tottrup et al. 2012). This agrees with ground records during spring migration, where Eleonora’s falcons have been observed hawking on large insects and perching on trees in Somalia following the rains (Walter 1979).

On occasions, upon reaching the Mozambique Channel in autumn, individuals have turned westwards towards Malawi before returning to cross for Madagascar. This delay in crossing could be attributed to unfavorable weather conditions, or alternatively an expected need to refuel before crossing over an ecological barrier (Alerstam 1978) within favorable feeding conditions, as found previously (Gschweng et al. 2008; Kassara et al. 2012). The suggestion though that this area can be considered as part of the wintering grounds of Eleonora's falcon (Gschweng et al. 2008; Kassara et al. 2017) is supported with our results here and deserves further investigation.

The remarkable non-stop flight by one of the individuals (Ifigeneia) for 3530 km in 85 hours, first to be recorded for Eleonora's falcon and one of the longest trips recorded for any species (Newton 2010a), indicates the capacity of Eleonora's falcon to travel extensive distances, over sea and other ecological barriers, such as deserts, without refueling. Lesser kestrels and Eurasian hobbies have been recorded flying up to 1626 and 740 km respectively, probably non-stop, during migration (Strandberg et al. 2009b; Limiñana et al. 2012), but Eleonora's falcon appears to be capable of much longer flights. Maximum recorded flight speeds amongst all individuals were typically over the Mediterranean Sea, the desert of Sinai and the Red Sea, mostly during the night in spring with a maximum recorded speed of 89 km/h.

While in accordance with previous studies, we suggest that the loop migration pattern is most likely attributed to habitat availability and the need for refueling (Kassara et al. 2012; Mellone et al. 2013), wind effect cannot be completely precluded. Our tagged individuals returned to the breeding grounds from routes east of the Red Sea, through the Arabian Peninsula, where tailwinds are favorable during that period, while headwinds might discourage a northwards Sahara crossing (Newton 2010a; Tottrup et al. 2012; NOAA 2017). We do not have sufficient data to investigate the effect of wind on migration, however, especially in spring. Nevertheless, multi-year monitoring provides us with a greater understanding of migration cycles (López-López et al. 2014) and our 4-year study is the longest telemetry study on Eleonora's falcon thus far. Apart from duration, this study is the first to use GPS-GSM transmitters on Eleonora's falcon, providing opportunities for more detailed information on migratory routes (Tomkiewicz et al. 2010), and allowing for more accurate explanations of bird migratory strategy in relation to vegetative cover and feeding opportunities (Klaassen et al. 2008; Guilford et al. 2011). More long-term migration studies with high accuracy transmitters, encompassing wind effect together with habitat preferences, will further contribute to our understanding of migratory strategies that in turn can better inform conservation efforts for long distance migratory birds during what is often the least well studied portion of their annual cycle (Klaassen et al. 2008; Hallworth and Marra 2015).

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CHAPTER 5

Phenology and daily activity patterns of wintering Eleonora's falcon

Phenology and daily activity patterns of wintering Eleonora's falcon*

ABSTRACT

Individually attached tracking devices on Eleonora's falcon from several colonies throughout the breeding range, recently confirmed suspicions that Madagascar is its almost exclusive wintering destination. Because of Madagascar's vast size, and Eleonora's falcon's global population of just 15000 pairs, observations of wintering indivuduals are scarcely reported in the literature. Advances in technology allowed us to use GPS transmitters, which provide data of greater spatial accuracy and finer temporal resolution than previously used satellite transmitters, thus allowing a more thorough investigation of the species wintering movements and habits. Our results suggest that during the wintering period Eleonora's falcon occupies extensive areas in Madagascar, moving progressively from more open areas towards areas with higher tree cover, and especially to humid forest, possibly as a response to spatiotemporal patterns in food abundance during the wintering period. Our data also indicate high intra-individual fidelity and relatively low connectivity. Time budget analysis revealed for the first time that Eleonora's falcons spend more than 80 % of their time resting or roosting, while just about 15 % of their daily activity is devoted to foraging, the latter being performed almost exclusively during the day. GPS transmitters highly enhanced our ability to understand the wintering ecology of Eleonora's falcon in Madagascar, allowing for more accurate habitat requirement identification and better spatiotemporal activity pattern identification.

Keywords: *Falco eleonorae*, Madagascar, telemetry, kernel, humid forest, tree cover, NDVI.

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INTRODUCTION

Long-distance migratory birds are susceptible to environmental pressures in different parts of the world, and thus may be more prone to population decline compared to sedentary species (Berthold 2001; Newton 2004; Sanderson et al. 2006). Wintering habitat deterioration can adversely influence breeding success through carry-over effects especially for insect feeders overwintering in Africa (Norris et al. 2004). Also, knowledge of the ecology of Afro-Palearctic migrant species at their wintering grounds, which can adversely affect subsequent life-cycle stages (Brown and Sherry 2006), is far less comprehensive than on breeding grounds (Sanderson et al. 2006; Kristensen et al. 2013) and the ecological factors impact upon wintering birds, apart from food, has been less documented (Sherry and Holmes 1996). New technologies including miniaturized GPS accuracy tracking devices allow for smaller species to be “followed” for short term studies e.g. at the breeding grounds (Guilford et al. 2008; Kotzerka et al. 2010). Long-term studies though to encompass wintering grounds for small and medium birds were thus far restricted with 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). GPS transmitter technology, combined with GSM data transmission was thus far restricted to larger bird species (Kendall and Virani 2012). Therefore, while individual tracking has provided substantial insight regarding breeding and migratory periods of raptors, we have much more to learn about their wintering ecology which has received thus far less attention (Trierweiler et al. 2013).

Eleonora’s falcon (*Falco eleonorae*) is a complete, trans-equatorial migrant species (Bildstein 2006; Pulido 2007; Kerlinger 2008), breeding primarily in the Mediterranean region and wintering predominantly in Madagascar (Walter 1979). It is a species with a restricted breeding and wintering range (Gschweng et al. 2008), thus it can be considered as a ‘double’ endemic (Bildstein 2006). It is considered amongst the most ecologically fine-tuned falcons (Cramp et al. 1980); its delayed breeding season coincides with passage of migratory birds over the Mediterranean Sea upon which it feeds during the offspring raising period, while its wintering period in Madagascar ensures abundance of insects upon which it feeds on the wing throughout the rest of the year (Del Hoyo et al. 1994). Eleonora’s falcon is listed within Annex I of the EU Directive 2009/147/EC, and requires special conservation measures to ensure its survival (European Parliament 2009). Nevertheless, necessary actions for habitat protection cannot be implemented due to the lack of detailed data on its year-round distribution (Mellone et al. 2013). Thus, further research is necessary, especially at the wintering grounds, to identify the species' ecological requirements, as well as to assess the presence of threats (Barov and Derhé 2011; BirdLife International 2015). The natural environment of Madagascar is threatened from intensive forest degradation (Walter 1979). Besides, it has been suggested that historic climate change might have already limited favorable habitats of Eleonora's falcon in Madagascar, including the possible shrinking of swamps and lakes, which are typically insect-rich (Walter 1979). While breeding populations of the species show an increasing trend (Birdlife International 2018), by contrast, wintering populations in Madagascar appear to be in decline (Thorstrom and Rene de Roland 2000); thus information on Eleonora's falcon habitat requirements, coupled with threat assessment are urgently required (Ristow and Bourdakis 1999; Barov and Derhé 2011; Mellone et al. 2012) for a proper appraisal of its global conservation status.

Direct observations (Thorstrom and Rene de Roland 2000; Zefania 2001) and bird ringing (Ristow and Wink 1995), have provided some indication of the species' presence in Madagascar. Nevertheless, Eleonora's falcon records in Madagascar are still rare (Walter 1979; Zefania 2001) and bird-habitat associations are challenging to make with fieldwork alone, because of the remoteness of areas within which the species mostly occurs (Walter 1979). But based on recent telemetry studies compiled in Kassara et al. (2017), through which it was confirmed that populations from throughout the breeding range almost entirely overwinter in Madagascar, habitats associations have been established at a broad scale. Detailed information though on spatiotemporal activity patterns and daily budgets has been completely lacking thus far (Gschweng et al. 2008; Gschweng et al. 2012; Kassara et al. 2012; Mellone et al. 2012; Kassara et al. 2014). Indeed, due to the relative positional accuracy of PTT transmitters used thus far, habitat relationships have been explored on a relatively broad scale, typically at 1 km^2. Nonetheless, these studies have shown that individuals tend to occur in heterogeneous areas, consisting of small and isolated patches of suitable habitat (Kassara et al. 2014); therefore, finer-scale studies would be needed for a better insight into species-habitat relationships. Daily activity patterns are also an important aspect to be considered in this respect, and to this end, flight speed can serve as an index of the species' behavior, with slower speeds observed during Eleonora's falcon foraging activity, compared with commuting flights (Hedenstrom et al. 1999). In spite of the finer tracking resolution that can be achieved using GPS accuracy tracking devices, the lack of detailed information on landscape structure is a critical limitation in exploring these species-habitat associations at finer scales.

Because many habitat variables are non-detectable in habitat mapping obtained through remote sensing (Tapia et al. 2007), ground-truthing related to the species ecology and habits still remains necessary and useful (Mack et al. 1997; Tapia et al. 2007). Indeed, structural features suitability of a habitat type to the specific bird species under study need to be verified to establish a relationship (Cody 1985), and habitat identification must fit species ecology (Garshelis 2000). Although broad scale remote sensing derived habitat mapping can be of high quality, as the resolution zooms-in, the accuracy suffers (Gottschalk et al. 2005; Moat and Smith 2007). Especially boundary definition and small patches of suitable habitats are likely to be misclassified (Rappole et al. 2003; Gottschalk et al. 2005). Drawing conclusions on remotely sensed habitats and their relation to birds involves user judgment and having statistically valid relationships, but not biologically meaningful, is not enough (Gottschalk et al. 2005). Ground-based mapping has better potential to explain bird species presence compared to remotely sensed habitat data, unless the scale is very broad (Mack et al. 1997). Thus, ground-truthing of the habitats used by Eleonora’s falcon in Madagascar as localized with telemetry is important especially for boundaries and patchy habitats and fragments (Kremen et al. 1999). Ground collected habitat data in combination with unbiased telemetry-obtained bird locations, is the most effective method to establish bird-habitat relationships, but cost is always a factor to consider (Gottschalk et al. 2005).

In this study, we identified the wintering areas of Eleonora’s falcons breeding in the Eastern Mediterranean with the use of both GPS and PTT data, identifying home ranges of tracked individuals breeding in Cypus and Greece. We also investigated fine-scale habitat relationships, including daily activity patterns and monthly movements, in relation to habitat characteristics (i.e. habitat type, tree cover, vegetation greenness and elevation), aided by ground-truthing of habitat types used by the species in Madagascar. This is the first study examining wintering ecology and behaviour of Eleonora’s falcon at such a fine scale, advancing substantially our knowledge of the species’ wintering ecology (Gschweng et al. 2012; Mellone et al. 2012; Kassara et al. 2014; Kassara et al. 2017), and allowing for a better evaluation of the threats and pressures the species faces in Madagascar.

MATERIAL AND METHODS

Field methods

Between 2009 and 2017 we monitored the year-round movements of Eleonora's falcons originating from Greece and Cyprus combining PTT (5 g and 9.5 g PTT transmitters, Microwave Telemetry) and GPS (GPS-GSM-UHF loggers, Ecotone Telemetry) technology. In 2013 and 2014, twelve birds were caught using mist nets close to their nests as well as at known foraging grounds at Akrotiri, Cyprus. Specifically, a mist net was placed on a cliff top opposite nests at the southern edge of the Akrotiri peninsula, with a taxidermic mount of Eagle owl (*Bubo bubo*) used as a decoy to lure falcons (Limiñana et al. 2012). In addition, four nets were set within an olive grove, where the falcons had been observed feeding on large beetles at dusk. Further data were obtained from two adult and two juvenile Eleonora's falcons captured at their nests in the central Aegean Sea in 2009 and fitted with PTT transmitters (see Kassara et al. 2012), as well as from another six adult Eleonora's falcons captured with mist-nets and fitted with GPS-GSM-UHF loggers at a known bathing location during the 2015 and 2016 breeding periods in the southern Aegean Sea. All 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. Birds were handled in accordance with standard procedures (Gosler 2004) and marked with metal rings (Redfern and Clark 2001), while biometric measurements including body mass were taken (Dawson 2004). No abnormal behavior 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-GSM-UHF loggers collected data every 4 hours on average (range 1 - 6 hours; hereafter, GSM data) and transmitted them via the GSM network. In addition the GPS-GSM-UHF loggers were also programmed to collect GPS data every 15 - 30 minutes. These GPS fixes (hereafter, UHF data) were stored in the loggers' memory and were retrieved for two falcons (one from Cyprus, CYPR03 and one from the Aegean Sea, ELEF02) via base station antenna placed close to nesting sites. Out of the 22 telemetry devices attached in total, 12 of them (6 GPS-GSM-UHF loggers and 6 PTT transmitters) provided wintering data (Table 1).

Table 1: Details of the satellite tracked individuals, recorded wintering events and number of retrieved locations during the wintering period

s/n	**Transmitter**	**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		1	466	7923		8389
7	ELEF04		1	693			693
8	ELEF05		1	775			775
9	94118	Central Aegean (Greece)	1			440	440
10	94119		1			502	502
11	94120		1			379	379
12	94121		1			617	617
		Total	**16**	**4879**	**12925**	**2828**	**20632**

Data filtering

The original dataset consisted of 20632 locations (Table 1), including GSM, UHF and PTT data. Due to a technical issue, one of the GPS-GSM-UHF loggers (CYPR03) did not transmit GSM data for about two months. We filled this gap by using the UHF data retrieved during the same period. In continuation, we filtered out locations received during the first and last seven days of each wintering event to account for migratory restlessness (Gschweng et al. 2012). After calculating pathmetrics, i.e. distance and time interval between consecutive points and subsequently travel speed, we also excluded those positions indicating 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 17740 positions in total.

We used PTT and GPS data (but for CYPR03, see above) 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 hour and 1 km apart to minimize spatiotemporal autocorrelation (Otis and White 1999; López-López et al. 2010;

Limiñana et al. 2012; López-López 2016; Kassara et al. 2017). For the habitat use analysis we also excluded PTT data of location classes LC1 and LC2. Furthermore, we explored the daily activity pattern of the two falcons for which UHF data were available, filtering out duplicates, as well as consecutive locations more than 1 hr apart.

Home range and site fidelity

To delineate the individual home ranges we used Utilization Distribution (UD) estimates, based on 95% and 50% probability fixed kernels (Worton 1989; Kassara et al. 2012; Limiñana et al. 2012; Trierweiler et al. 2013; Kassara et al. 2014). We then assessed site fidelity by estimating the intra-individual and inter-individual overlap, based on the Utilization Distribution Overlap Index (UDOI), which accounts for the overlap in space as well as for the probability distribution within the intersected area (Fieberg and Kochanny 2005). For one individual (ELEF02) we had data coverage for one complete season with GSM and UHF data, thus we were able to compare the effectiveness of the two systems in home range estimation. All analyses were carried out in R v3.4.4 (R Core Team 2018), using the 'adehabitatHR' package (Calenge 2006).

Daily activity

We explored daily activity patterns, including day and night differences in behaviour, using nautical dawn and dusk to assign the path segments to day and night, thus accounting for the crepuscular ecology of the species (Walter 1979; Cramp et al. 1980). We classified each path segment into four activity types judging by their corresponding speed, namely commute (> 20 km/h), forage (1 – 20 km/h), and rest / roost (< 1 km/h during day / night, respectively). Given that for one of the two falcons (namely, CYPR03) the UHF data did not cover the entire wintering period, we first investigated whether there were differences in their daily activity patterns by comparing the duration of each activity type during the overlapping period via Mann-Whitney U tests. Subsequent analyses were run for each individual separately to account for inter-individual variability. We calculated the Spearman correlation coefficient between all possible pairs of activity types. We also investigated hourly distribution of foraging activity during the day using χ^2 tests. We assessed the relationship between night-time foraging activity and moon phase, by computing the Spearman correlation coefficient between the duration of night-time foraging events and the illuminated fraction of the moon separately. Moreover, we explored differences in habitat preferences (based on percent tree cover, elevation and NDVI; see below for a description on remotely sensed data acquisition) between daytime forage and rest and nighttime forage and roost, using Mann-Whitney U tests. We also calculated the percentage of time devoted for foraging during day and night for each individual. For the individual whose UHF data covered the entire wintering period (namely, ELEF02) we also explored seasonal patterns in the duration of each activity type by calculating their partial correlation coefficient with Julian date controlling for day length. Activities were split on date change, to get equal 24 hour periods for daily time budget calculations, as well as on transitions between day and night and vice versa to compare day and night time-budgets. Statistical analyses were carried out in SPSS v20.0.0 (SPSS 2011), spatial analyses in ArcGIS 10.1 (ESRI 2012), while sunlight and moon phases were computed in R v3.4.4 (R Core Team 2018), using the 'suncalc' package (Agafonkin and Thieurmel 2018).

Seasonal patterns in habitat use

We explored spatiotemporal patterns of areas used by the tracked individuals taking into consideration the habitat types of the Madagascar vegetation mapping project (Moat and Smith 2007), vegetation phenology using the Normalized Difference Vegetation Index (hereafter, NDVI) (NASA 2018), percent tree cover using the Vegetation Continuous Field (hereafter, VCF) (NASA 2018) and elevation (USGS 2016). The spatial resolution of these layers was much coarser than the accuracy of GPS data and similar to the accuracy of the PTT LC3 data that was used in this analysis. Specifically, the resolution was for habitat type: 250 x 250 m, NDVI: 250 x 250 m, VCF: 250 x 250 m, and elevation: 150 x 150 m.

We used Mann-Whitney U tests to examine progressive change in values of VCF, elevation and NDVI, with monthly windows as a grouping factor (actually 32-day windows to cover two NDVI 16-day granules – Table 2), comparing each window with its successive one. NDVI, in contrast to VCF and elevation, is constantly changing as the wintering season progresses, thus, in addition to the above analysis, we used paired t-tests to compare the average NDVI value of the positions occupied during each 32-day period, with the average NDVI during the same period, but at the positions occupied during the previous and subsequent 32-day periods by the birds. Using this analysis, we could compare the NDVI at the present location with what NDVI would have been available if the birds rather than moving to the current locations occupied, instead stayed in their previous locations, or alternatively moved 32 days earlier to the positions occupied during the next 32-day window. This analysis was performed to gauge whether the birds move from wintering site to wintering site to maximize NDVI. Progressive habitat use was examined using binomial mixed models in Stata 11.0 (StataCorp 2013). For each frequently used habitat type (i.e. cultivation, western dry forest, plateau grassland – wooded grassland mosaic, wooded grassland – bushland, humid forest and degraded humid forest), we run the model after assigning to it the value of one and the value of zero to all the others, with individual as a random effect and the 32-day windows as a grouping factor. We excluded though the first and last 32-day windows as they were underrepresented in both number of days and number of individuals present. Analysis was similarly repeated with all possible combinations of habitat types.

Table 2: Date ranges for 32-day windows used in analyses, each incorporating two consecutive 16-day NDVI granules (NASA 2018)

32-day windows	Dates
1	16 October – 16 November
2	17 November – 18 December
3	19 December – 16 January
4	17 January – 17 February
5	18 February – 21 March
6	22 March – 22 April
7	23 April – 24 May

On-site habitat mapping and threat identification

The Madagascar vegetation mapping project is considered the most accurate vegetation mapping available so far for Madagascar (Mellone et al. 2012) with a usable resolution of 250 x 250 m (Moat and Smith 2007). However, a more refined mapping would have been useful (Bibby 2000) to match the spatial accuracy of the GPS data we obtained (< 20 m) (Ecotone 2013). In addition, because of the complexity of landscape composition due for example to fragmentation, and given ongoing habitat changes in Madagascar where land-use changes and deforestation are intensive (Grinand et al. 2013; Kassara et al. 2014), ground-truthing was deemed essential (Gottschalk et al. 2005; Tapia et al. 2007). We thus identified clusters of locations based on GSM and PTT LC3 data that were available by spring 2015 encompassing areas of under 5 km^2 (Tapia et al. 2007). We initially selected 27 concentrations from which we filtered out nine as inaccessible and targeted a total of 18 sites, of which we aimed to reach at least ten to ground-truth habitat. In April 2015 we performed an on-site habitat assessment to map the habitat types, as well as to identify and assess potential threats. In spite of limitations in available time and accessibility of some sites, with much flooding and road damage throughout Madagascar following the rainy season, we nevertheless managed to ground-truth 10 sites.

High-resolution satellite imagery was used during the on-site habitat mapping as this allowed for the distinction between e.g. degraded and intact forest, and allowed for preparatory draft outlining of the habitat types (Grinand et al. 2013). These images were printed with a coordinates grid overlay (Bibby 2000). A target point within each site was reached and confirmed by using a handheld GPS. Since our goal was to assess the reliability of the Madagascar Vegetation Mapping Project (Moat and Smith 2007) in finer spatial scale, we retained the same classification scheme as much as possible, and added subcategories where necessary to enable more efficient analysis (Bibby 2000), including habitat features matching the ecology of the species and reflecting its preferences (Bibby 2000; Ausden 2004). On-site habitat types were identified and drawn on the image, by using delineation lines, aided by GPS readings where necessary (Bibby 2000; Sutherland et al. 2004). Hand-drawn maps were then digitized in ArcGIS 10.1 (ESRI 2012). We compared differences between the Madagascar Vegetation Mapping Project habitat types with the results of the on-site mapping exercise, to identify any discrepancies between the existing mapping and the actual conditions on the ground. During the field surveys, we also assessed any human and natural threats present at each site visited (Bibby 2000; Sutherland et al. 2004). Each identified threat received a score from 0 – 3 to characterize the extent and intensity of the threat. We estimated the impact of any given threat by summing the scores for its extent and intensity and subsequently calculating their relative impact on a 1 – 100 scale.

RESULTS

Home range and site fidelity

All tracked individuals in this study spent their winter exclusively in Madagascar, primarily roaming in the eastern part of the island (Fig. 1). Home range size based on 95% kernels for each wintering event had an average size of 14399 km^2 (SD = 7307 km^2), ranging from 3540 km^2 to 31537 km^2 (Table 3), while home range overlap between wintering events (UDOI values) are presented in table 4. Mean intra-individual overlap for those individuals tracked in multiple wintering seasons, was 0.80 (SD = 0.49, N = 4) for CYPR03 and 1.03 (2 years) for CYPR01. For one of the individuals we had both GSM and UHF data for the entire wintering season (ELEF02), the home ranges were practically identical resulting in a UDOI of 2.15. The mean UDOI overlap among all individuals was 0.04 (SD = 0.10), while inter-colony overlap between birds tagged in Greece and in Cyprus was on average 0.01 (SD = 0.04). Within colony overlap was 0.002 (SD = 0.006) and 0.09 (SD = 0.13) for Cyprus and Greece respectively.

Daily activity

The two individuals from Greece and Cyprus that provided UHF data, appeared to have similar daily budgets, dedicating about 80 % of their time either to resting (day) or roosting (night) and approximately 15 % to foraging (Fig. 2 and Table 5). For both individuals time spent foraging was positively correlated with time devoted to commuting trips (ELEF02: r_s = 0.439, P < 001, N = 152; CYPR03: r_s = 0.340, P = 0.025, N = 43), and negatively correlated with resting time (ELEF02: r_s = -0.806, P < 001, N = 152; CYPR03: r_s = 0.740, P < 0.001, N = 43). Controlling for day length, the individual we had a complete wintering event appears to have progressively decreased the duration of commuting trips (partial r_s = -0.192, P = 0.018, N = 149) and increased the duration of resting time (partial r_s = 0.273, P = 0.001, N = 149), while the duration of roosting did not vary throughout the wintering season (partial r_s = 0.067, P = 0.416, N = 149). For both individuals the duration of foraging was significantly higher during the day than during the night. Specifically, 93.4% of time spent foraging occurred during day-time for ELEF02 and 97.7% for CYPR03. Time spent foraging during the day decreased over the wintering period for ELEF02 (partial r_s = -0.238, P = 0.004, N = 146).

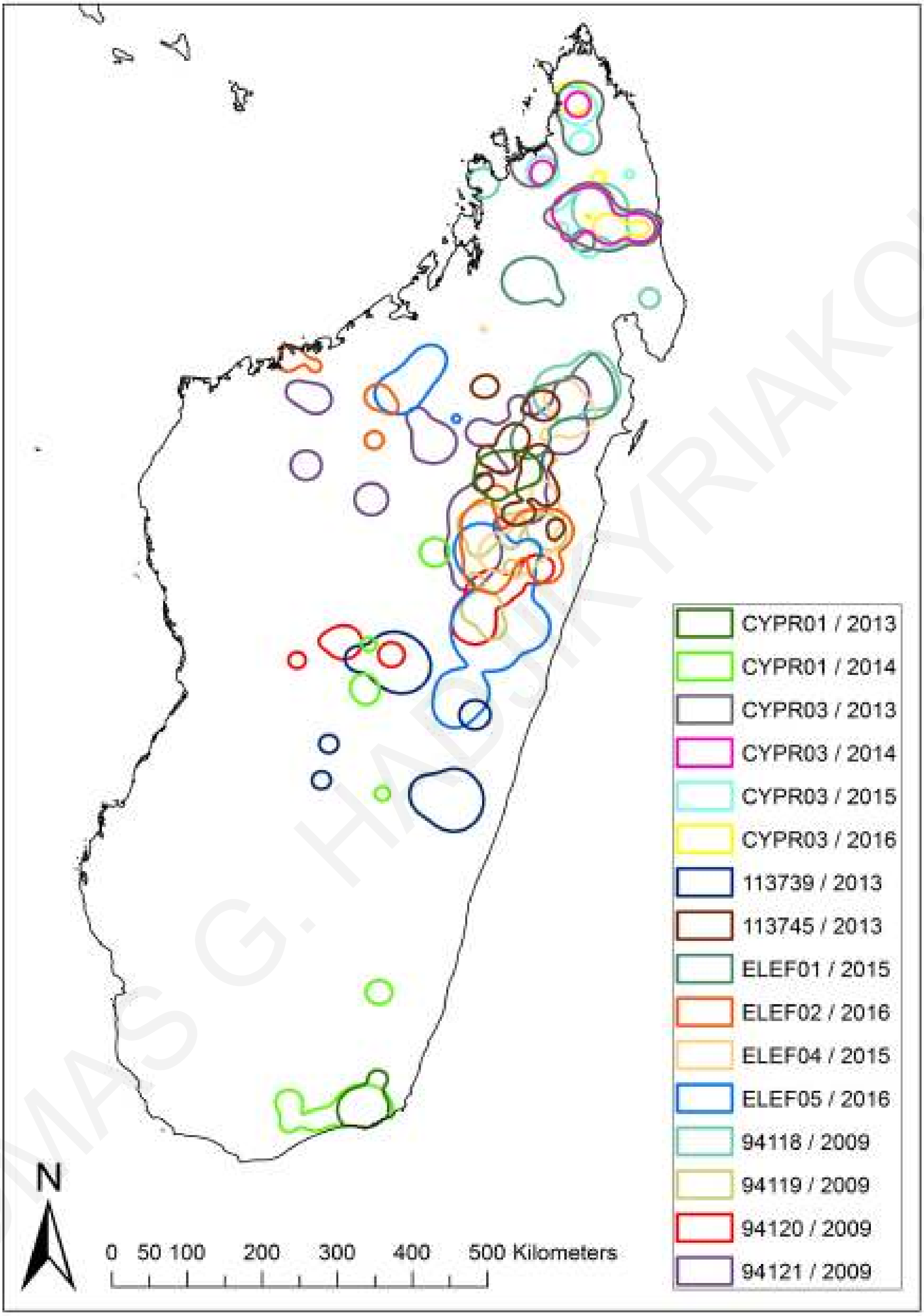

Figure 1: Home ranges (95% kernels) of tracked individuals for each wintering event, illustrated on an outline map of Madagascar (European Commission 2015).

Table 3: 95% kernel estimates (UD) for tracked individuals during each wintering event

Individual	**Wintering event**	**Data reception**	**Number of locations**	**95% kernel area (km^2)**
CYPR01	2013 - 2014	GSM	86	7777
CYPR01	2014 - 2015	GSM	113	10072
CYPR03	2013 - 2014	GSM	530	15775
CYPR03	2014 - 2015	GSM	1667	7940
CYPR03	2015 - 2016	GSM	527	11190
CYPR03	2016 - 2017	GSM	242	3540
ELEF01	2015 - 2016	GSM	610	13330
ELEF02	2016 - 2017	GSM	385	15434
ELEF02	2016 - 2017	UHF	3187	16324
ELEF04	2015 - 2016	GSM	620	11107
ELEF05	2016 - 2017	GSM	660	27440
113739	2013 - 2014	PTT	163	13920
113745	2013 - 2014	PTT	196	10034
94118	2009 - 2010	PTT	63	13487
94119	2009 - 2010	PTT	188	9285
94120	2009 - 2010	PTT	134	9745
94121	2009 - 2010	PTT	249	31037
			Mean	14399
			SD	7307

Table 4: Home range overlap (UDOI) results for tracked individuals during the wintering period

Individual / Wintering event	94118 / 2009	94119 / 2009	94120 / 2009	94121 / 2009	113739 / 2013	113745 / 2013	ELEF 01 / 2015	ELEF 02 / 2016	ELEF 04 / 2015	ELEF 05 / 2016	CYPR 01 / 2013	CYPR 01 / 2014	CYPR 03 / 2013	CYPR 03 / 2014	CYPR 03 / 2015
94119 / 2009	0.00														
94120 / 2009	0.00	0.09													
94121 / 2009	0.01	0.07	0.00												
113739 / 2013	0.00	0.00	0.01	0.00											
113745 / 2013	0.01	0.00	0.00	0.11	0.00										
ELEF01 / 2015	0.25	0.00	0.00	0.04	0.00	0.09									
ELEF02 / 2016	0.00	0.47	0.02	0.13	0.00	0.00	0.00								
ELEF04 / 2015	0.10	0.04	0.00	0.11	0.00	0.01	0.06	0.45							
ELEF05 / 2016	0.00	0.11	0.35	0.04	0.00	0.00	0.00	0.13	0.03						
CYPR01 / 2013	0.00	0.00	0.00	0.02	0.00	0.03	0.00	0.00	0.00	0.00					
CYPR01 / 2014	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.03				
CYPR03 / 2013	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
CYPR03 / 2014	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.16		
CYPR03 / 2015	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.23	1.29	
CYPR03 / 2016	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.17	0.62

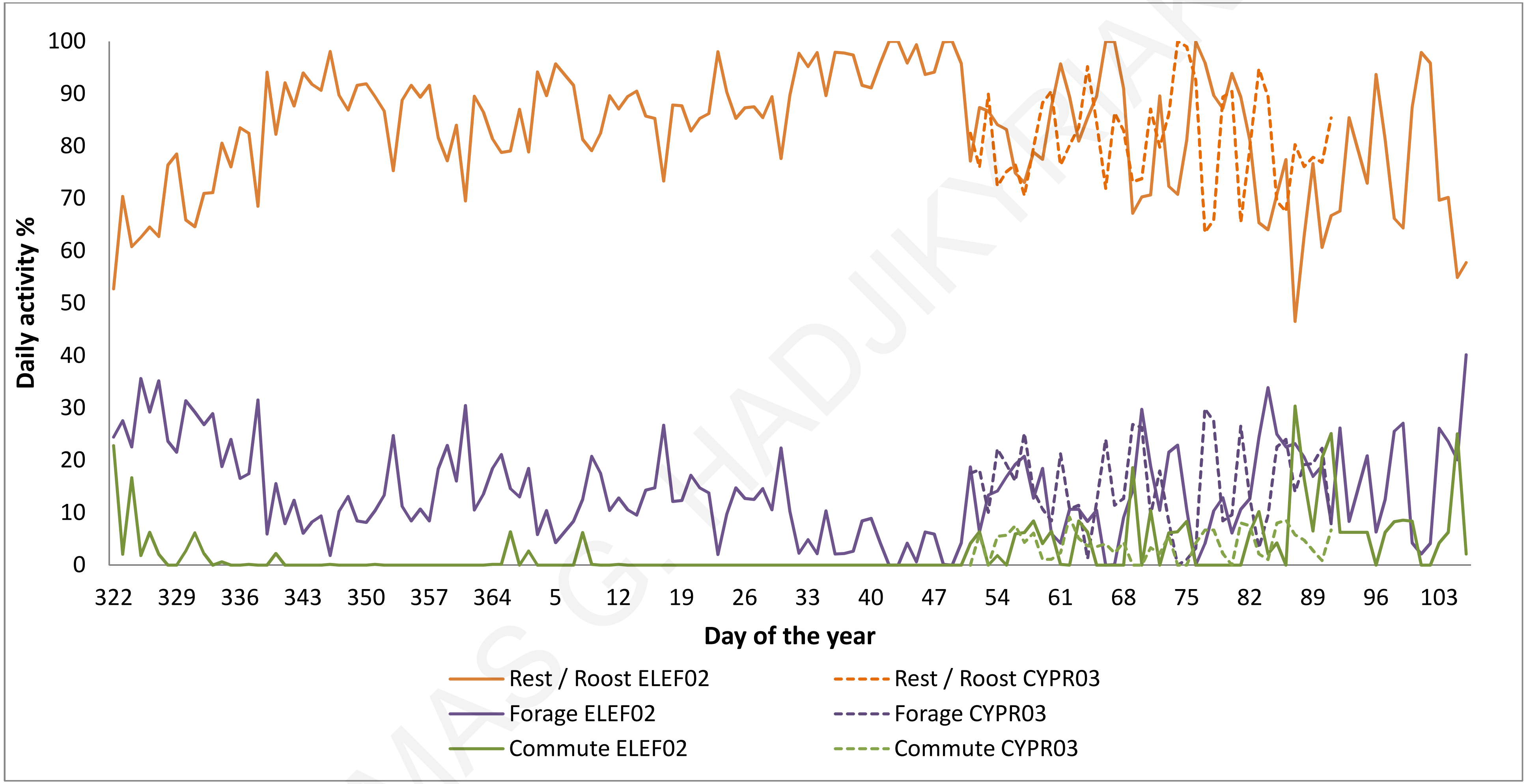

Figure 2: Daily activity patterns (roost is combined with rest) for the two individuals with UHF data, indicating a similar pattern for the same time of year (data for the two individuals are from different years).

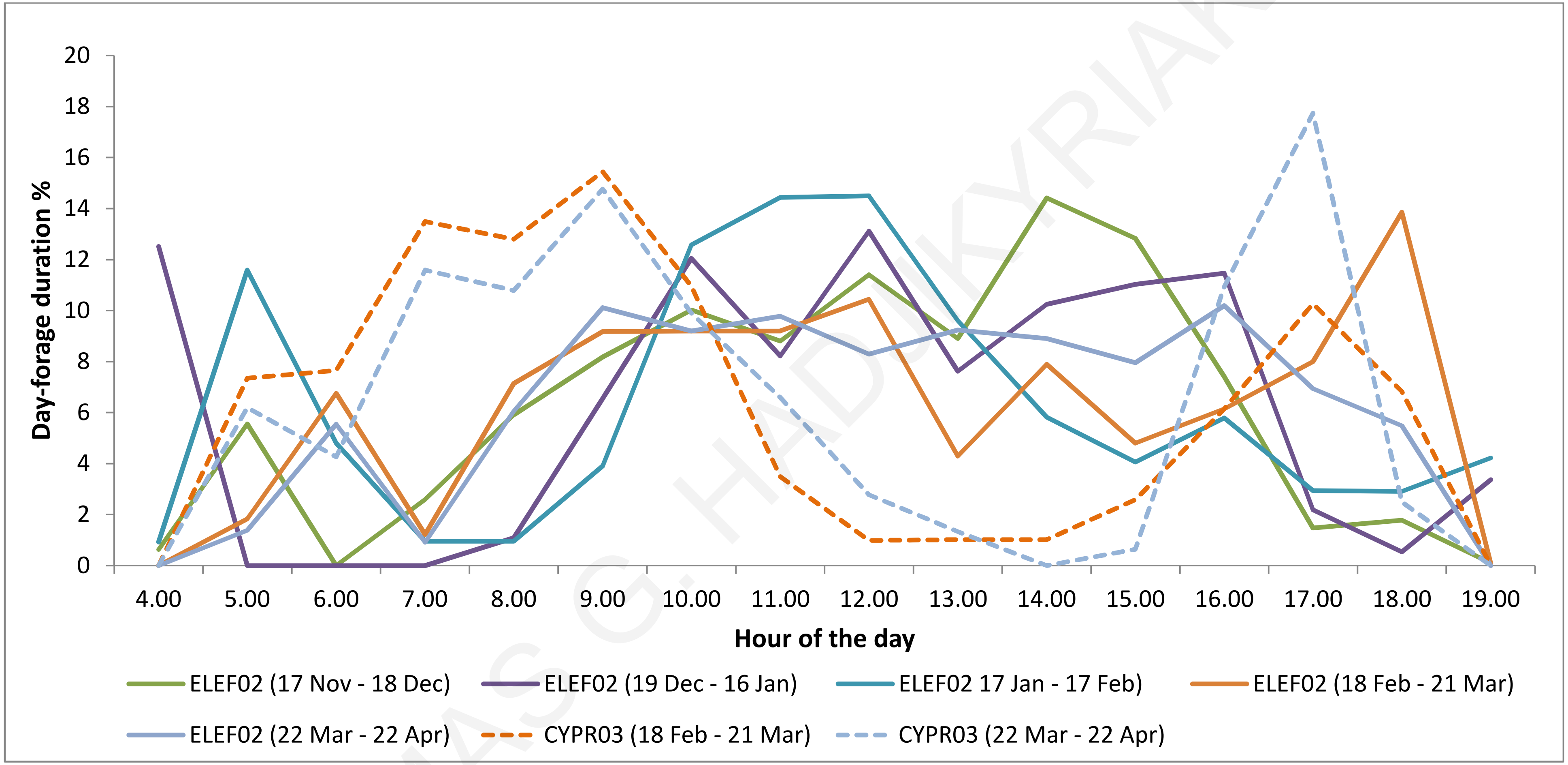

Figure 3: Hourly distribution of foraging activity during daytime (expressed as a percentage), grouped in 32-day windows. ELEF02 differs from CYPR03 in concentrating its foraging effort during the middle of day, whereas CYPR03 tends to rest in the middle of the day and is more active in the early morning and late afternoon. This pattern appears consistent for both individuals throughout the winter.

Table 5: Daily time budget (expressed as a percentage) for two individuals with UHF data. Results are similar for both falcons apart from higher resting time for ELEF02

Activity type	**CYPR03 2014**		**ELEF02 2016**		**Mann-Whitney U test between activity of ELEF02 / 2016 and CYPR03 / 2014 (during same time period)**	
	mean	SD	mean	SD	U	p
Commute	4	3	3	5	882.00	0.582
Forage	16	10	14	9	799.50	0.215
Rest	39	14	44	12	857.50	0.016
Roost	41	12	39	7	875.00	0.547

There were significant differences between the daytime foraging frequency per hour of the day for both individuals (ELEF02: χ^2 (15) = 290.39, P < 0.01; CYPR03: χ^2 (13) = 254.97, P < 0.01). ELEF02 appears to forage at any hour between typically 09:00 – 16:00, while CYPR03 exhibits a bimodal foraging pattern, which peaks during the morning and afternoon hours (Fig. 3). Daytime foraging for CYPR03 occurred in areas with higher tree cover, elevation and NDVI, than found in resting, while for ELEF02 daytime foraging occurred in areas with higher elevation, and lower NDVI than found for resting (Table 6). Nighttime forage though, occurred in areas with higher NDVI and tree cover only for ELEF02, than found in roosting, while for CYPR03 there was no significant difference in any of the three habitat characteristics tested (Table 6). Contrary to expectations, the duration of night foraging was negatively correlated with moon fraction for ELEF02 (r_s = -0.290, P = 0.025, N = 60) and the same negative relationship was observed for CYPR03, yet not statistically significantly (r_s = -0.449, P = 0.226, N = 9).

Table 6: Comparison of habitat characteristics in areas used for foraging and resting/roosting for day and night respectively, for two individuals with UHF data

	ELEF02				**CYPR03**			
	Daytime forage vs rest		Nighttime forage vs roost		Daytime forage vs rest		Nighttime forage vs roost	
	Z	P	Z	P	Z	P	Z	P
Elevation	-12.12	< 0.001	-1.284	0.199	-21.29	< 0.001	-0.303	0.762
VCF	-0.42	0.674	-2.867	0.004	-24.17	< 0.001	-1.028	0.304
NDVI	-4.47	< 0.001	-2.971	0.003	-10.83	< 0.001	-0.129	0.898

Seasonal patterns in habitat use

There was a progressive change in percent tree cover (VCF) over the course of the wintering season (Fig. 4a), with tracked individuals moving progressively to areas with increasingly more tree cover (Table 7). Between 32-day windows 2 and 3, birds moved to lower elevations, until they moved between windows 4 and 5 to significantly higher elevations, where they remained until the end of the wintering season (Table 7, Fig. 4b). NDVI increased throughout the season (Table 7, Fig. 4c), though this was an artifact of NDVI increasing over time throughout the rainy season, as shown by comparing same-period NDVI among areas occupied by individuals during the previous and subsequent time windows with areas occupied during the current window (Fig. 5, all comparisons P > 0.05, except for window 2). A progressive change in habitat type occupied over time was clearly evident (Fig. 4d), with a decreasing trend in time spent in cultivations, western dry forest, plateau grassland – wooded grassland mosaic and wooded grassland – bushland, and an increasing trend in time spent in humid forest and degraded humid forest (Table 8).

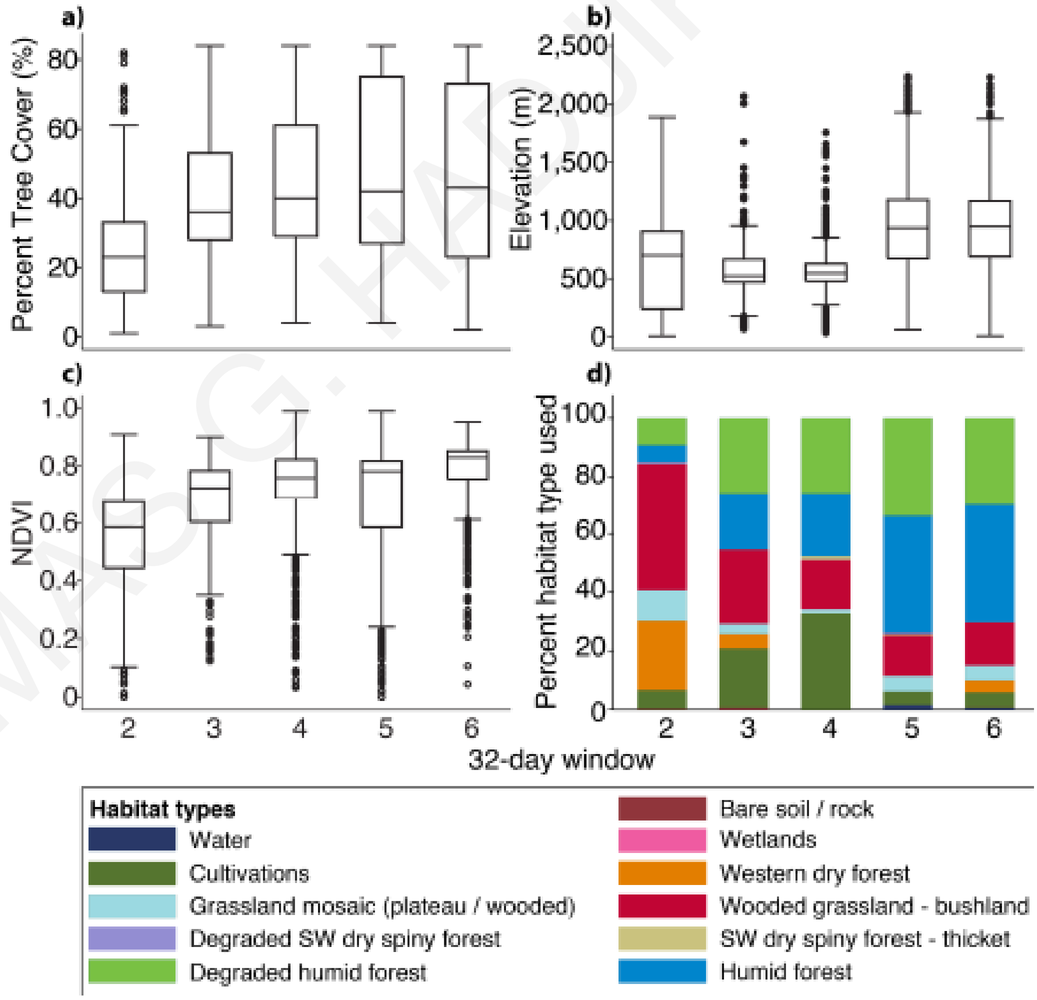

Figure 4: Progressive change over the course of the wintering season (in 32-day windows) in a) percent tree cover; b) elevation; c) NDVI and d) percent habitat type used (from Madagascar vegetation mapping project – see legend below figure for habitat types).

Table 7: Tests for the progressive change in the locations of the tracked individuals in percent tree cover (VCF), elevation and NDVI during the course of the wintering season (comparing successive 32-day windows).

Variable	Days window 2 – 3 (N = 1731)		Days window 3– 4 (N = 1671)		Days window 4 – 5 (N = 2664)		Days window 5 – 6 (N = 2873)	
	Z	P	Z	P	Z	P	Z	P
VCF	-17.56	< 0.001	-4.99	< 0.001	-3.65	< 0.001	2.10	0.003
Elevation	4.45	< 0.001	0.035	0.97	-29.43	< 0.001	-0.47	0.64
NDVI	-13.78	<0.001	-7.85	<0.001	-0.62	0.053	-13.75	<0.001

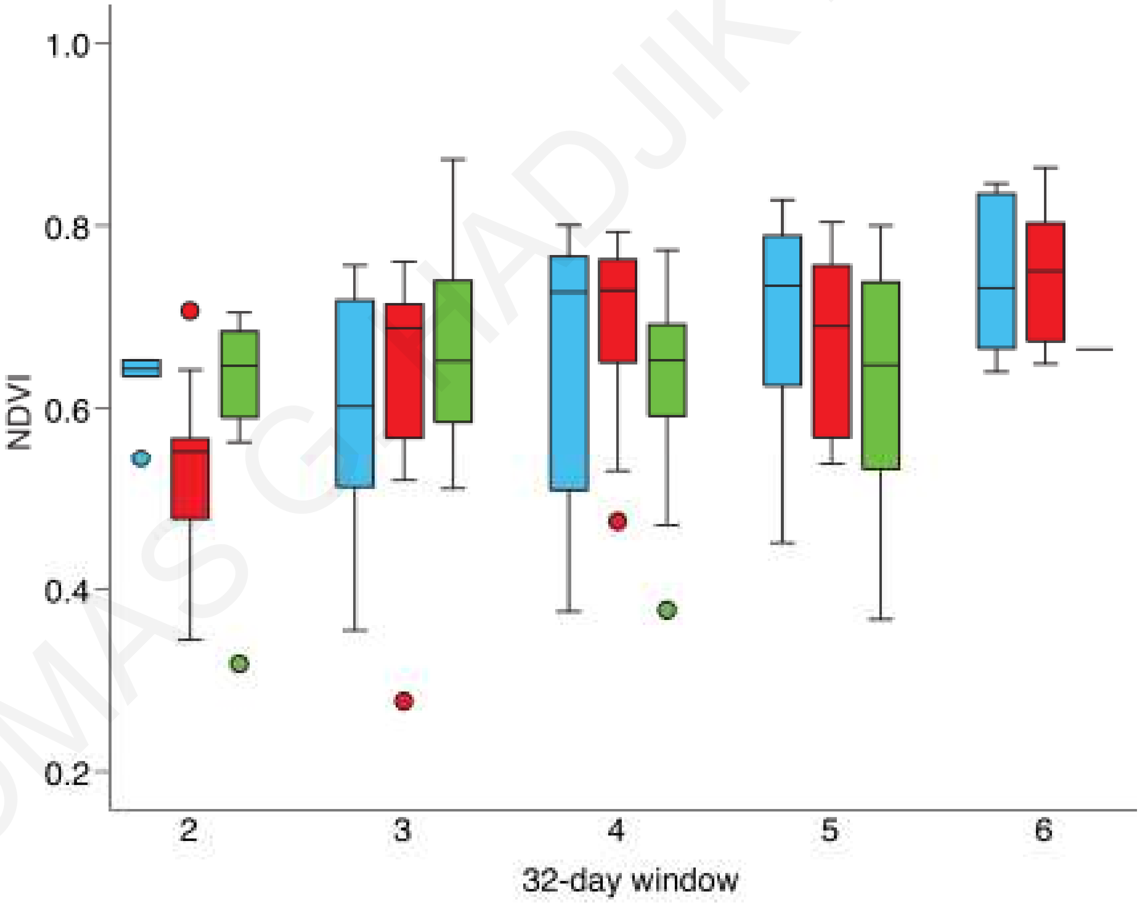

Figure 5: Comparison of actual NDVI values (red columns) over the course of the wintering season (in 32-day windows), compared with the NDVI of the same period in the areas that tracked individuals were in 32 days earlier (blue columns) and 32 days later (green columns).

Table 8: Binomial mixed models test results for habitat type presence over time during the course of the wintering season (in 32-day windows). Negative coefficient values indicate progressive decrease while positive coefficient values indicate progressive increase in habitat usage

Habitat type	**Coefficient**	**SE**	**Z**	**P**
Cultivation	-0.2273	0.0308	-7.37	< 0.001
Western dry forest	-0.9809	0.0581	-16.89	< 0.001
Plateau / wooded grassland mosaic	-0.1741	0.0452	-3.86	< 0.001
Wooded grassland - bushland	-0.4187	0.0260	-16.07	< 0.001
Degraded humid forest	0.2834	0.0245	11.55	< 0.001
Humid forest	0.4585	0.2438	18.81	< 0.001

Table 9: Comparison of Madagascar vegetation mapping project habitat types with ground-truthed habitat types in Madagascar using locations from four tracked individuals

Madagascar vegetation Mapping Project habitat types (bold font) vs ground-truthing habitat types (plain font)	**Number of bird locations**
Humid forest	**6**
Grassland with scattered trees	1
Intact humid forest	5
Plateau grassland-wooded grassland mosaic	**8**
Eucalyptus plantation	2
Grassland with scattered trees	5
Mixed cultivations	1
Western dry forest	**68**
Intact western dry forest	41
Western dry forest with openings	27
Wooded grassland-bushland	**37**
Eucalyptus plantation	2
Grassland with scattered trees	16
Intact humid forest	2
Intact western dry forest	2
Mixed cultivations	3
Wooded riverine	12

On-site habitat mapping and threat identification

On-site habitat mapping revealed some discrepancies between the habitat types presumably used based on the Madagascar vegetation mapping project (Moat and Smith 2007) and the actual habitats surveyed (Table 9). Although there was an overall agreement at the scale that the Madagascar vegetation mapping project was prepared (250 x 250 m), small patches of certain habitat types, mostly man-made, such as cultivations and plantation forests (e.g. rice fields and eucalypt plantations) were not distinguished (see Fig. 6). Overall, field surveys revealed that the greatest threats to used habitats were human-induced changes in land-use, primarily annual crop intensification, clear felling, fire, and firewood collection (Table 10).

Table 10: Threats for Eleonora's falcon in Madagascar identified during field work, with their relative calculated impact

Threat	**Relative impact (scale 1-100)**
Firewood collection	15.1
Annual crop intensification	13.8
Clear felling	13.7
Fire	13.0
Charcoal production	7.2
Chemicals	5.7
Selective felling	5.0
Eucalyptus plantation	4.9
Irrigation infrastructure	4.9
Grazing	4.6
Intensive forest management	4.1
Perennial crop intensification	2.9
Pine plantations	2.1
Floods	1.3
Timber collection	1.1
Poaching	0.5
Total	**100.0**

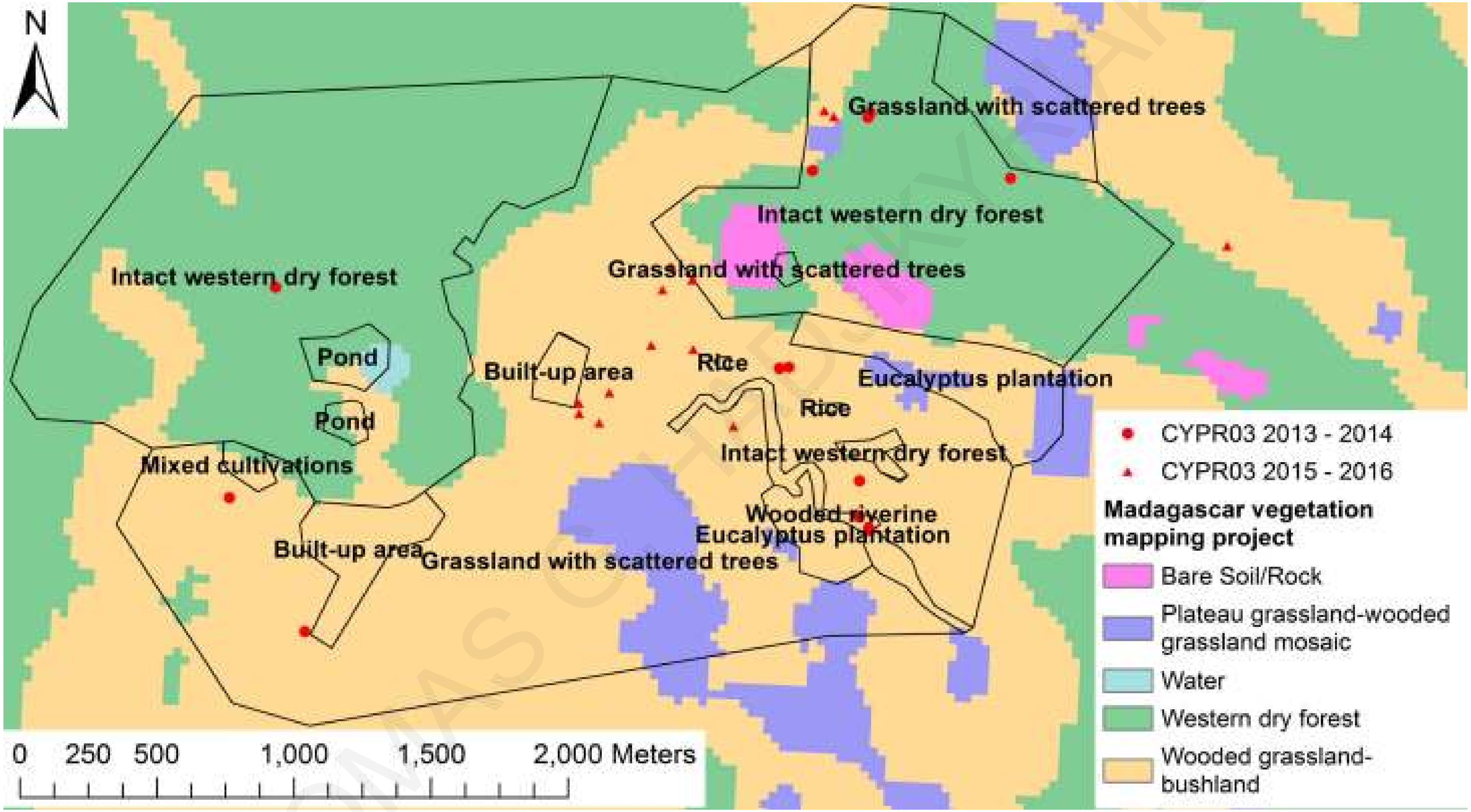

Figure 6: Habitat type example comparison between Madagascar vegetation mapping project (coloured raster with legend) and ground-truthing habitat mapping (black polygons outlines with habitat type names within them), for area surveyed at Ankarana National Park area in northern Madagascar.

DISCUSSION

For the first time we were able to determine daily activity patterns of Eleonora's falcon in Madagascar and estimate daily time budgets during day and night. This was possible by utilizing the dense collection pattern of UHF data, combined with their high positional accuracy, which was not possible in previous work using PTT data only, for which data for day and night had to be pooled (Mellone et al. 2012). Both individuals providing us with UHF data appear to have similar time budgets across activities, allowing us to a certain extent to generalize our results and draw conclusions on the activity of Eleonora's falcon in Madagascar. Most of the time-budget is devoted to rest during the day and roost at night, involving 19 – 20 hours of the 24 hour time-budget, similarly with ferruginous hawks at their wintering grounds (Plumpton and Andersen 1997), while foraging is accomplished in 3.5 hours on average per 24 hours, almost exclusively distributed during daytime (between nautical dawn and dusk), in contrary to previous findings (Buij and Gschweng 2017). Nevertheless we found evidence for some nighttime foraging activity and again, contrary to expectations and previous work (Cramp et al 1980; Buij and Gschweng 2017), we found a negative correlation of its occurrence with moon phase. We suggest that previously found significant nighttime activity of Eleonora's falcon in Madagascar (Buij and Gschweng 2017) might be due to the temporal limitations of PTT transmitters, which only allowed the description of the frequency of nighttime activity rather than duration, yet without testing the statistical significance of the observed correlation of night foraging with the moon phase. Time spent foraging is not surprisingly correlated with time spent in commute flights, as individuals need to commute to reach their foraging areas. Time spent roosting, which takes place during the night, does not vary during the winter, after controlling for variation in day length, but time spent foraging during the day decreases progressively, suggesting individuals require less time to forage once they've move to their core wintering areas, of humid forest at higher elevations. This indicates that they may be able to quickly satisfy their dietary requirements with less effort (Brandt and Cresswell 2009) when they can forage close to and within the humid forest where the abundance of insects is expected to increase as the rainy season progresses (Wolda 1978). Foraging activity actually occurs in more vegetated areas, at higher elevations, where rainfall is higher and consequently they may be able to find more insects there, compared to the more open areas where the birds rest and roost.

In raptors, prey availability is associated with habitat type (Tapia et al 2007). At first, field-based studies investigating the wintering range of Eleonora's falcon (e.g.

Zefania 2001), suggested that any habitat type was suitable, including natural and human altered habitat types such as cultivations and secondary forests, as long as there was an abundance of flying insects. In contrast to field-based studies, satellite telemetry studies provide unbiased localisation data unaffected by accessibility in the field (Kassara et al 2017), thus allowing for the identification of remote areas in which Eleonora's falcons overwinter (see Kassara et al. 2017). Such telemetry studies revealed a preference for intact and degraded humid forest in areas with high elevation and rainfall, but suggested they especially prefer fragmented patches of forest (Kassara et al 2014). Thus, while areas used by Eleonora's falcon were predominated by pristine humid forest, it has been suggested that it is actually degraded humid forest and cultivations that were preferred within those areas, while grasslands and intact humid forest were mostly avoided (Mellone et al. 2012), except that they might hunt over pristine forest, but overall they preferred forest edges (Mellone et al. 2012). Habitat associations in previous studies were performed mostly with remotely sensed data for Madagascar, and have included using data from the Madagascar vegetation mapping project (Moat and Smith 2007), and vegetation greenness (NDVI) as a proxy for food availability (Gschweng et al. 2012; Kassara et al 2014; Kassara et al. 2017). High rainfall over the rainy season with the associated progressive increase in vegetation greenness is expected to stir up an abundance of large insects especially in the rainforest and at forest edges (Wolda 1978). Our results from GPS telemetry and ground surveys suggest that upon its arrival in Madagascar, Eleonora's falcon initially spends time in wooded grasslands and bushlands, as well as in western dry forests. It then occupies more open areas including cultivations at lower elevations, before gradually moving towards the humid forest, either intact or degraded, at much higher elevations, and this is especially the case during the last two-three months of its time at its wintering grounds. Although previous work has suggested individuals track changes in NDVI and seek habitats with higher NDVI levels (Gschweng et al. 2012), our results show that NDVI actually increases uniformly over the rainy season in areas occupied by Eleonora's falcon, with no evidence that they move from place to place chasing higher NDVI. Instead, we found that they change their tree cover and habitat type, and associated elevation preferences over the course of the wintering period. In general, habitat usage in raptors is temporally variable (Tapia et al 2007). Movements of Eleonora's falcons in the winter seemed to follow a serial residency pattern (Creswell 2014), with transition between geographically distinct areas as the wintering season progresses. These multiple centers of activity might be following seasonal changes e.g. in rainfall which in turn cause seasonal changes in food (insect) availability (Catry et al. 2011; Kassara et al 2014). Humid forest and cultivations (Wolda 1978), as well as forests with openings, might indeed provide an abundance of insects (Fuentes-Montemayor et al. 2013; Hahn and Orrock 2015), but the rainy season in tropical areas of Madagascar peaks typically between December and February (Moat and Smith 2007; Grinand et al. 2013; Ghimire et al. 2017), which then triggers greater seasonal insect activity in the humid forest (Wolda 1988). Falcons are likely more successful at foraging for prey in more open, drier habitats prior to the peak of the rainy season, as they are used to do on their breeding grounds, but then move to their core wintering areas as the rainy seasons kicks in to take advantage of the abundance of insects over the humid forest (Wolda 1988).

To test our bird-habitat associations we were able to map in high detail some of the activity areas of the species, showing that at a broad scale, the Madagascar vegetation mapping project reflects the habitat present on the ground. It was evident though that at a finer scale, species may occupy more open areas than what was indicated through the Madagascar vegetation mapping project. In particular, we found that many GPS-localised positions were from forest with extensive openings, rather than in extensive closed canopy forest, in grassland with scattered trees rather than wooded grassland and in more extensively cultivated areas as well. 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, reinforcing our assumption that before the rainy season kicks in they may hunt insect prey more easily in open areas such as grasslands and cultivations (Zefania 2001), though single or scattered trees and forest patches were still important for roosting and resting in these open habitats.

The main threats identified primarily within the activity areas visited during fieldwork in Madagascar were human induced habitat disturbance and management, including extensions of cultivated areas and irrigation infrastructure, especially for rice – the staple of the Malagasy diet, forest degradation and extension of woody plantations such as eucalypts (Vagen 2006), timber and fuelwood collection including charcoal production, and fire including slush and burn. Intensification of slush and burn (tavy) and shortening of the fallow cycles, highly contributes towards humid forest degradation and fragmentation of Madagascar humid forests (Styger et al. 2007). Direct threats to the species, such as poaching, are of less concern. But activities such as extensive spraying for locust elimination (Kassara et al. 2017) can have a direct impact as the insect feeding ecology of Eleonora’s falcon is adversely affected when insects are limited, and on the other hand, poisoning can be a threat as at the breeding grounds (Xirouchakis 2004). Deforestation in Madagascar is progressing at an alarming rate and it is expected that forests will only eventually remain on the highest mountains (Green and Sussman 1990). The extensive deforestation that occurred in the early 20th century, changing the landscape of Madagascar (Jarosz 1993), might have had an impact on overwintering Eleonora's falcon. Ongoing deforestation is rampant and includes the reduction of remaining pristine forest as well as fragmented forest (Harper et al. 2007). At the same time, more open habitats containing forest remnants and scattered large trees are important for the perches they provide (Cody 1985, Lihu et al. 2007), with more than 80% of the birds' time spent resting (day) or roosting (night). Even planted trees can serve as perches but the observed short interval felling, does not allow trees to grow sufficiently to fulfill that purpose, thus conserving large native trees such as Mango is important (Sherry and Holmes 1996).

The tagged individuals in our study exclusively overwintered in Madagascar, in areas matching the habitat suitability predicted by distribution models (Gschweng et al. 2012; Kassara et al. 2017). Intra-individual home range overlap was very high, suggesting high site fidelity, while by contrast, inter-individual home range overlap was very low, in agreement with previous work (Kassara et al. 2017), especially for the individuals tagged in Cyprus, which occupied areas all along the eastern half of Madagascar. Our findings contradict the assumption of Gschweng et al. (2012) that absence from predicted areas in the south was potentially because of population specific preferences. As shown previously by Kassara et al. (2017), inter-colony overlap was higher than intra-colony overlap with falcons from Greece and Cyprus exploiting to some extent the same areas, consistent with a migratory connectivity pattern of high spread, e.g. of over 1300 km for individuals tagged in Cyprus, and high mixing (Cresswell 2014; Finch et al. 2017).

The extended home range size of Eleonora's falcon in Madagascar, precludes 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), and which has required a high number of observers in the field (Craig et al. 1988). In spite of the challenges presented by Eleonora's falcon phenology in Madagascar, we managed to obtain for the first time detailed spatiotemporal data on its wintering ecology including its daily activity patterns at an hourly rate, habitat usage during the day and at night as well as monthly patterns of progressive movements and associated changes in habitat preferences. This was possible through the use of GPS-GSM-UHF loggers, with high spatial accuracy and high temporal frequency that provided us with the opportunity to associate environmental information with bird locations in remote areas with pinpoint accuracy (Hallworth and Marra 2015). In general, the accuracy of GPS loggers is an indispensable tool in understanding species ecology, particularly in the tropics, where habitat loss is the primary threat to raptor species (Bildstein 2006).

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CHAPTER 6

Synopsis

Synopsis

This study covered the annual cycle of Eleonora’s falcon, a long-distance migrant species exposed cumulatively to multiple threats at different places far away between them, involving both hemispheres of the planet. Eleonora’s falcon breeds in the Mediterranean and overwinters in Madagascar, crossing the Equator twice a year. Using high accuracy transmitters and novel techniques, combined with fieldwork at both ends of the species reach, i.e. Cyprus and Madagascar, I was able to study the population of Eleonora’s falcon breeding in Cyprus, combining where possible my results with those from groups working on the species in Greece and beyond to include the entire breeding range west to the Canary Islands. In general I conclude that:

1) The Eleonora’s falcon population in Cyprus comprised about 130 breeding pairs exhibiting a stable trend, while breeding success was 1.54 ± 0.85 fledglings per breeding pair. Breeding success levels were on par with those from the rest of the Eastern Mediterranean and considerably higher than previous estimates for Cyprus.

2) Only a fraction of the nesting sea-cliffs at Akrotiri colony has physical characteristics that render it as highly suitable for nesting. Early breeders were more successful, whilst repeatedly used nests had a higher breeding output. The timing of the breeding period was congruent with other colonies in the Aegean Sea.

3) Between pairs cannibalistic behaviour was video-recorded for the first time in Eleonora’s falcon, with a female adult taking a nestling from a neighbouring nest to feed its own offspring. As this behaviour is difficult to witness, its role in hatchling loss in colonial raptor species needs to be further examined.

4) Use of advancing technology such as drones, photogrammetry, GIS, photography and videography (e.g. camera traps), combined with traditional ones such as boat and ground surveys, can highly enhance the assessment of population status in colonial bird species and can produce results that would otherwise require higher effort and resources.

5) Individuals from Cyprus migrated to Madagascar covering more than 7000 km twice a year. They exhibited a loop migration pattern flying west of the Red Sea in autumn and

east of it in spring. Intra-individual route fidelity was found to be strong on consecutive trips both temporally and spatially.

6) Tracked individuals flew quickly during day and night over the sea and the desert with flight speeds up to 89 km/h; one remarkable continuous flight covered 3530 km in 85 hours. As soon as they were over vegetatively rich areas, they slowed down and roosted during the most nights.

7) Individuals flew through more vegetated areas than what is available to them, which provided them with refuelling opportunities, either by fly-and-forage or at selected stopovers.

8) Individuals from the Eastern Mediterranean occupied areas all along the Eastern Madagascar, spreading over distances of more than 1300 km between them. Intra-individual site fidelity was also identified at wintering grounds, with almost identical home ranges calculated from year to year.

9) Upon their arrival in Madagascar, Eleonora's falcons moved through more open habitats with less tree cover, such as grassland and cultivation, but progressively moved into areas with denser tree cover and elevation, especially in humid forest, either intact or degraded.

10) Daily activity at the wintering grounds suggested that individuals were able to satisfy their daily intake by devoting just 3 – 4 hours to foraging, while they rested and roosted for the majority of their daily activity cycle, with very little time devoted to foraging at night.

11) The use of GPS accuracy positions obtained through GPS-GSM-UHF loggers provide opportunities for fine scale analysis of spatiotemporal movements of medium size raptors at an hourly rate, highly enhancing the potential for establishing bird-habitat associations in remote areas.

12) Ground-truthing provided detailed information on habitat usage, allowing for better interpretation of remotely sensed habitat data associations with telemetry-obtained bird locations and better assessment of potential threats to species and habitats.

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APPENDIX I

Hadjikyriakou, T.G. and Kirschel, A.N.G., 2016. Video evidence confirms cannibalism in Eleonora’s falcon. Journal of Raptor Research, vol. 50, no. 2, pp. 220-223

APPENDIX II

Kassara, C., Gangoso, L., Mellone, U., Piasevoli, G., **Hadjikyriakou, T.G.,** Tsiopelas, N., Giokas, S., Lopez-Lopez, P., Urios, V., Figuerola, J., Silva, R., Bouten, W., Kirschel, A.N.G., Virani, M.Z., Fiedler, W., Berthold, P. and Gschweng, M., 2017. Current and future suitability of wintering grounds for a long-distance migratory raptor. Scientific Reports, vol. 7, no. 1:8798