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Wintering habitats of Eleonora's Falcons *Falco eleonorae* in Madagascar

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Capsule Eleonora's Falcons wintering in Madagascar selected degraded humid forests and cultivated areas close to pristine humid forest.
Aims To identify the habitat preferences of Eleonora's Falcon *Falco eleonorae* on their wintering grounds in Madagascar, and to use this information to gain insights into the conservation priorities of this species.
Methods A total of 11 Eleonora's Falcons were captured in Spain in 2007 and 2008 and equipped with solar-powered satellite transmitters. We obtained information on five complete wintering events for three birds, two of them tracked for two consecutive years. Data were analyzed using geographic information system-based cartography.
Results The analyses showed a preference for degraded humid forests and cultivated lands within areas where pristine humid forests were the most abundant habitat type.
Conclusions Eleonora's Falcons could be taking advantage from a spill-over edge effect of their insect prey into cultivated and more open areas close to humid forests. However, the importance of humid forests for Eleonora's Falcons seems to be high. The current loss of this habitat in Madagascar is a cause for concern with respect to the conservation of this long-distance migratory falcon species.

A consistent body of recent literature suggests that, in contrast to resident bird species, populations of migratory species can be affected by events occurring in different parts of the world (Newton 2004). Moreover, it has recently been shown that populations of long-distance migratory birds are declining at a faster rate than short-distance migrants or resident species (Sanderson *et al.* 2006). Therefore, understanding the interactions between different periods of the annual cycle in migratory birds becomes of the greatest importance for their conservation (Martin *et al.* 2007, Bowlin *et al.* 2010).

Eleonora's Falcons *Falco eleonorae* are long-distance migratory raptors, which breed mainly in islands of the Mediterranean Sea and winter mainly in Madagascar (Walter 1979). The species is listed in the Annex I of the Directive 2009/147/EC and constitutes a priority species for conservation (BirdLife International 2010). Unfortunately, long-term series of comparable demographic data are lacking, but on the basis of recent surveys, the species seems to be stable or steadily increasing across its whole distribution range (Del Moral 2008, Dimalexis *et al.* 2008). Although the migratory routes have recently been mapped in detail (Gschweng *et al.* 2008, López-López *et al.* 2009, López-López *et al.* 2010, Mellone, López-López *et al.* 2011), little is known about the species' habitat requirements on its wintering grounds. Such information is key for the conservation of Eleonora's Falcons, since actions for habitat preservation, especially at wintering grounds, remain largely unimplemented (BirdLife International 2010).

Our knowledge of the ecology of migratory birds has been constrained by the difficulties in tracking individuals across seasons. Several methods such as traditional ringing and banding have been employed in recent decades (Berthold 2001). Nevertheless, advances in the miniaturization of satellite tracking devices are now making it possible to determine the connections between the different seasonal grounds of birds in a

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way unimaginable few years ago (Wikelski *et al.* 2007). Other methods, such as genetic markers, stable isotopes (Hobson 2008) and geolocators (Rodríguez *et al.* 2009), although complementary, do not allow fine-tuned habitat selection analyses that are possible with satellite tracking. Nevertheless, wintering-focused analyses performed with this technology have received little attention in comparison with the greater body of research dealing with migratory routes, and hence very few studies have been published so far (Gerkmann & Meyburg 2009, Jiguet *et al.* 2011).

The island of Madagascar has been identified as one of the most important biodiversity hotspots in the world, which is strongly endangered owing to several threats – mainly habitat loss, including deforestation (Myers *et al.* 2000, Harper *et al.* 2007, Irwin *et al.* 2010). In this context, the identification and conservation of optimal habitats for long-distance migratory species that winter in Madagascar is of the utmost importance. Besides benefits for the species itself, it could be useful also for wider conservation aims, given that raptors prove to be, in certain conditions, good biological indicators (Sergio *et al.* 2005, 2008). With the aim of identifying habitats where conservation actions should be focused, we analyze here the habitat preferences of Eleonora's Falcons wintering in Madagascar. According to the International Action Plan for the species, the location of the wintering areas and the description of their ecological characteristics are urgently needed and have been considered an 'essential' priority (BirdLife International 1999, 2010).

METHODS

Study species

Eleonora's Falcons are colonial raptors, which breed mainly on Mediterranean islands, from Spain to Greece, including several islands located in the central Mediterranean (Italy), and the northern coast of Africa (Algeria and Libya) (Walter 1979). They also breed in a few colonies located in the Atlantic Ocean, including the Canary Islands (Spain) and Mogador (Morocco). The bulk of the population (80–90%) breeds in Greece (Dimalexis *et al.* 2008). Winter records are almost exclusively restricted to Madagascar (Walter 1979, Gschweng *et al.* 2008, Kassara *et al.* 2011), although some observations (mainly juveniles) have been recorded on the eastern coast of Africa (Kenya, Tanzania and Mozambique) (Gschweng *et al.* 2008, authors unpubl. data). Since individuals belonging to different populations concentrate in such a narrow winter range, a comprehensive mapping and a complete description of habitat requirements at wintering areas is crucial in order to gain insight into conservation priorities for the species as a whole. In fact, to the best of our knowledge, only sporadic visual observations of Eleonora's Falcons in Madagascar have been reported so far (Thorstrom & René de Roland 2000, Zefania 2001). In this context, information based even on a small sample size of tracked birds could be useful, at least as a starting point for further investigations, which could be also applied to fieldwork planning.

Animal tagging and transmitter terminal programming

A total of 11 Eleonora's Falcons were trapped in Balearic (39°30′N 3°00′E) and Columbretes Islands (39°55′N 0°40′E), located in the western Mediterranean (Spain) (Fig. 1). Birds were trapped in autumn 2007 and 2008, and were equipped with Microwave Telemetry Inc. 9.5-g solar-powered transmitter terminals (López-López *et al.* 2009, López-López *et al.* 2010). During the wintering season, transmitters were programmed to collect data (coordinates, date and time) on a duty cycle of 12 hours on/58 hours off. Since the transmitters provide data of different accuracy, only high-quality locations (location classes 1–3; maximum error < 1 km) were used for the analyses (Soutullo *et al.* 2007).

Here, we only used wintering data from those individuals for which we recorded the complete wintering season (between arrival on the wintering grounds and the onset of the following pre-breeding migration). We used data belonging to three adult individuals, two of them tracked for two consecutive years (i.e. five different wintering events). Locations obtained less than one hour after the previous one were excluded from the analyses to avoid spatial autocorrelation and, when more than one location was available within an hour, we used the one of highest quality (Limiñana *et al.* 2008). On average, each wintering event accounted for 235 locations (range: 187–286, $n = 5$) spanning from November to April.

Habitat preferences and kernel estimation

To map the wintering areas in detail, we estimated the individuals' home-range core area of every wintering event through fixed kernel density contours (*sensu* Worton 1989), using the Animal Movement Extension

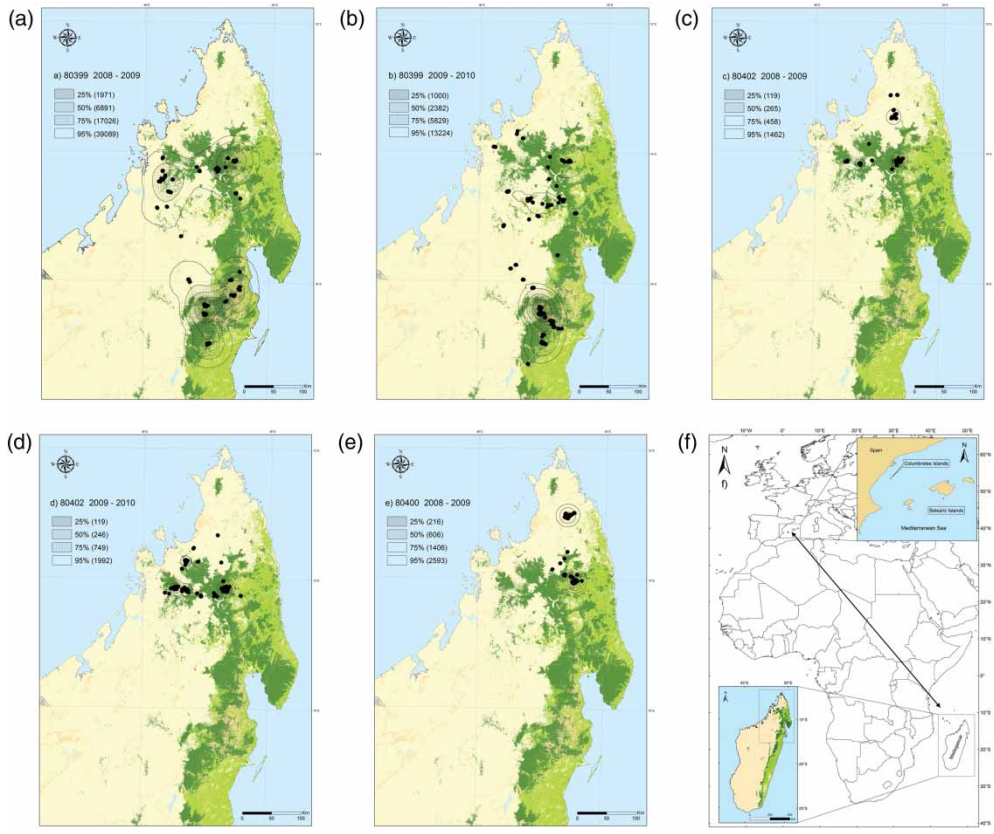


Figure 1. (a–e) Wintering locations (•) of three Eleonora's Falcons tracked by satellite-telemetry in northern Madagascar. Range sizes (km^2) according to kernel density contours for five wintering events are as follows: (a) individual #80399, wintering event 2008/09; (b) #80399, wintering event 2009/10; (c) #80402, wintering event 2008/09; (d) #80402, wintering event 2009/10; (e) #80400, wintering event 2008/09. Dark green area represents humid forest, while pale green area represents degraded humid forest (following Moat and Smith [2007]). (f) Location of Eleonora's Falcon's tagging sites in the western Mediterranean and the wintering areas in Madagascar.

for ArcView, version 3.2 (Hooge & Eichenlaub 2000). We calculated the 25%, 50%, 75% and 95% fixed kernels using the least-squares cross-validation (LSCV) procedure (Silverman 1986). We chose the 50% kernel to represent the core areas after a detailed exploratory analysis, since it represents a reasonable trade-off between including a sufficient number of locations excluding outliers and, moreover, it allows comparisons with similar studies (Mellone, Yáñez *et al.* 2011). In our case, nearly 60% of overall locations were included within the core areas (range: 42–93%; Fig. 1). To assess individual fidelity to the wintering grounds, we calculated the inter-year overlap of the core areas of the two birds tracked during consecutive years. In order to describe habitat composition of wintering areas, we calculated the percentage of every habitat type within the core areas for each one of the five wintering events separately, using the geographic information system layers produced by the Madagascar Vegetation Mapping Project (http://www.vegmad.org). These layers are based on the combination of remote sensing technology and field data collected by expert botanists (2003–06), and are the most accurate vegetation maps of Madagascar that are readily available (Moat & Smith 2007). Despite the ongoing changes in land cover in the country, it is unlikely that it could alter our results, owing to the short time-lapse between map compilation and the collection of our falcon tracking data. In fact, the deforestation rate of Madagascar forests has decreased from the beginning of the 1990s, in comparison with previous decades (Harper *et al.* 2007). We performed a habitat selection analysis to check whether Eleonora's Falcons occurred more frequently in certain habitats than expected by chance. To this end, we calculated a minimum convex polygon (MCP) for each wintering event (thus, three for the first year and two for the second one), which represents the maximum extension of available habitat, from which

birds actively select the preferred habitats (Worton 1995). We then generated 1000 randomly distributed points within each one of the five MCPs using 'Hawth's analysis tools' for ArcMap 9.2 (Beyer 2004), and assigned a habitat class to every random point, as well to as every real recorded location. To determine whether a bird preferred any particular habitat we used Monte Carlo tests (Manly 1997) to compare the observed frequency of real locations in different habitat types with the expected ones (Cadahía *et al.* 2010). The expected frequencies were obtained by sampling 1000 times, the same number of real bird locations from the list of random locations (Soutullo *et al.* 2008). Each individual wintering event was analyzed separately to avoid statistical pseudoreplication and no analysis including all the five wintering events at the same time was conducted. In addition, the analyses were first carried out for diurnal and nocturnal locations separately. Since the results did not differ between diurnal and nocturnal locations, we then pooled day and night data for further analyses, and here we present the results based on the complete data set. Monte Carlo analyses were conducted using Excel's PopTools 3.1 (Hood 2010). Pair-wise comparisons were two-tailed and the critical alpha level was set at $P < 0.05$.

RESULTS

Eleonora's Falcons' wintering areas were located in northern Madagascar (Fig. 1), where birds spent about five months of the year. Taking into account the core areas (50% fixed kernel contours), birds used one or two areas each wintering season (Fig. 1), with a median overall area of 606 km^2 (range: 246–6891 km^2, $n = 5$; Table 1). The two birds tracked during two consecutive wintering seasons used areas in their second year that they had used in the previous year, indicating site-fidelity. Bird #80399 used a smaller area during the second year that was completely within the one used in the first year (Fig. 1). On the other hand, bird #80402 used areas of similar size in both years (Table 1), with an overlap of 78.4% (Fig. 1).

Humid forest was the most abundant habitat within the core areas (pooling all data: 52.4% of the total surface area; Table 1). Habitat selection analyses showed that within individuals' MCPs, Eleonora's Falcons actively selected some habitat types, showing preferences for degraded humid forests and cultivations ($P < 0.005$ in the five cases; Table 1) and avoiding grasslands and humid forest ($P < 0.008$ in the five cases; Table 1). Furthermore, a detailed inspection of maps showed that birds selected degraded humid forests and cultivated areas close to pristine humid forests (Fig. 1).

DISCUSSION

Wintering habitats of Eleonora's Falcons

Our results show that Eleonora's Falcons wintered in northern Madagascar, and were mostly located on the humid eastern slopes of the island, rather than on the dry western ones (Moat & Smith 2007) (Fig. 1). The eastern region of Madagascar is amongst the highest areas of the country, which accounts for the high rainfall levels that occur there. In tropical rainforests, higher rainfall levels may result in high numbers of insects (Wolda 1978) and consequently, falcons may select these sites rather than dry lower areas of the island owing to higher insect prey availability.

Eleonora's Falcons showed clear winter site-fidelity in consecutive years. Although this finding is based on a small sample size (two birds in only two consecutive years), our results are in agreement with previous reports concerning other raptor species during the wintering season (Alerstam *et al.* 2006, Strandberg *et al.* 2008, García-Ripollés *et al.* 2010, Limiñana *et al.* 2011), which suggest that falcons select areas at least in part on the basis of knowledge acquired in previous years. In addition, all three individuals used approximately the same area during the first wintering season (Fig. 1), which might suggest some degree of bird association during winter. This is in agreement with Zefania (2001), who reported Eleonora's Falcons associating in groups of 3–21 in Madagascar. These results, together with those of individuals tracked from other populations (Sardinia and Greece) which spent the winter in northern Madagascar (Gschweng *et al.* 2008, Kassara *et al.* 2011), suggests that our findings are consistent across years and might be applied to a larger proportion of Eleonora's Falcons during the wintering season in Madagascar. These results also suggest that the strength of migratory linkages (i.e. migratory connectivity) between breeding ranges and wintering grounds among different European populations of Eleonora's Falcon should be the subject of future research.

Within the core wintering areas roughly half of the habitat was pristine humid forest. However, results of habitat selection analyses showed an active preference by Eleonora's Falcons for degraded humid forest and cultivated areas (Table 1).

Table 1. Extension of the distinct habitats (km^2) encompassed within the 50% kernel contours and significance levels of the habitat selection analysis (Monte Carlo tests) of three Eleonora's Falcons during five wintering events in Madagascar.

Individual ID	80399						80400			80402						Total	
Wintering event	2008/09			2009/10			2008/09			2008/09			2009/10				
Habitat	Area	%	*P*	Area	%	*P*	Area	%	*P*	Area	%	*P*	Area	%	*P*	Area	%
Water	1	0.01	x	0	0.00	x	0	0.00	x	0	0.00	ns	0	0.00	ns	1	0.01
Bare soil/rock	0	0.00	x	0	0.00	x	2	0.26	0.400	0	0.00	0.001	0	0.00	ns	0	0.00
Cultivation	1099	15.95	0.001 (+)	223	9.35	0.001 (+)	114	18.72	0.001 (+)	22	8.34	0.001 (+)	18	7.21	0.005 (+)	1362	13.92
Western dry forest	0	0.00	0.001	0	0.00	ns	8	1.33	0.007	0	0.00	ns	0	0.00	ns	0	0.00
Plateau grassland – wooded mosaic	152	2.21	0.001 (–)	40	1.70	0.001 (–)	65	10.78	0.001 (–)	1	0.48	0.001 (–)	1	0.34	0.001 (–)	195	1.99
Wooded grassland – bushland	708	10.28	0.001 (–)	377	15.81	0.006 (–)	73	12.05	0.001 (–)	10	3.67	0.001 (–)	8	3.22	0.002 (–)	1102	11.27
Wetlands	26	0.38	ns	14	0.59	0.017	0	0.00	x	0	0.00	ns	0	0.00	0.001	40	0.41
Humid forest	3538	51.34	0.001 (–)	1348	56.63	0.001 (–)	103	17.03	0.001 (–)	113	42.48	0.001 (–)	125	50.56	0.008 (–)	5123	52.36
Degraded humid forest	1367	19.83	0.001 (+)	379	15.92	0.001 (+)	242	39.83	0.001 (+)	120	45.03	0.001 (+)	95	38.67	0.001	1961	20.04
Total	6891	100		2382	100		606	100		265	100		246	100		9784	100

+, habitat is selected; –, habitat is avoided; significances are neglected when the given habitat had less than ten observed locations; x, habitat was not represented in any random point of the corresponding wintering event.

The pristine humid forests of Madagascar are multilayered evergreen woodlands with a canopy that can reach 30–35 m high. Since the 1970s, 33.4% of this forest has been destroyed, and repeated clearing has often made regeneration impossible. Currently, 39% of the area of pristine forest is formally protected (Moat & Smith 2007). The structure and ecology of degraded humid forests varies enormously, ranging from nearly intact forest to wooded grassland open areas (Moat & Smith 2007).

Our results showed that Eleonora's Falcons selected degraded humid forests close to pristine humid forests. Although we cannot rule out the possibility that falcons hunt within pristine forests, our results suggest that they prefer forest edges, where they could perhaps be benefiting from a spill-over edge effect of prey insects. This could make these ecotonal areas more profitable for prey capture, with pristine humid forests acting as a source of prey (Rand *et al.* 2006) and the adjacent areas acting as sinks (Gibson *et al.* 2011).

In agreement with our findings, Bildstein (2006) stated that migratory raptors wintering in the neotropics prefer edges and second-growth forests, rather than large pristine ones (Morel & Morel 1992) and, even within Madagascar, Watson *et al.* (2004) observed a 'significantly greater number of raptors on the edge of the littoral forest than in the core'. It is likely, therefore, that the patches of pristine forests surrounded by a matrix of open areas could be exploited by Eleonora's Falcons, especially the edges between these two types of habitat. Finally, the results also showed a slight preference for cultivated areas, probably rice fields, where flying insects are abundant and easy to catch (Zefania 2001).

Conservation implications

It has been suggested that the loss of wintering habitat could negatively affect a population even more than the loss of breeding habitat (Sutherland 1996). Thus, conservation efforts addressed only to one season or stage of the life-cycle of this long-distance migratory species may be inefficient, being jeopardized by threats occurring in ranges completely different from the breeding ones (Martin *et al.* 2007).

Our results suggest that the primeval humid forests of Madagascar and the close-by ecotonal areas are the most important habitat for Eleonora's Falcons during the wintering season. The findings of the present study should be of concern in the light of the rapid decline of humid forests in Madagascar, which could disappear by 2067 according to current predictions (Moat & Smith 2007). Our findings, although based on a limited sample, fill an important gap in the knowledge of the ecology of Eleonora's Falcons and could be used to focus conservation efforts and further field studies. In a global context, pristine forests currently attract the strongest protection efforts (Bermingham *et al.* 2005, Gibson *et al.* 2011), but our results, which are in agreement with other recent research on the value of tropical secondary forest (Chazdon *et al.* 2009), show that second growth forests, peripheral and ecotonal areas, especially when close to more pristine areas, deserve attention for the conservation of Eleonora's Falcons.

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