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## Influence of habitat and nest-site quality on the breeding performance of Lanner Falcons *Falco biarmicus*

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**Abstract.** Site quality may influence breeding performance especially in raptors showing strong territory fidelity as predicted by the site-dependent population regulation hypothesis. Thus, the occupancy of nest-sites is non-random, indicating a preference of certain territories, apparently of higher quality. During four breeding seasons (2003–2006), we recorded the occupancy rate and the number of young fledged from Lanner Falcon *Falco biarmicus feldeggii* nest-sites in eastern Sicily, Italy. Breeding sites with different occupancy rates showed significant differences in environmental attributes, mainly altitude. A generalised linear model revealed a significant effect of the slope of the nest-site on mean fledgling number per successful pair. In addition, the mean slope of the nest territory and the slope of the nest-site are the main predictors for differentiating the cliff selection by Lanners and by much more competitive Peregrine Falcons *Falco peregrinus*. Finally, our results suggest a crucial role of the high quality sites for the population viability. Occupancy rates were positively related to the mean number of young fledged per territorial pair and during the four years of the study period six high quality nest-sites raised 58% of young produced in the whole study area. We suggest that the annual production of young of the high quality territories should be preserved and that evaluation of the effective contribution of the low quality sites for the persistence of a viable population in Sicily should be performed.

**Key words:** territory quality, occupancy, *Falco biarmicus feldeggii*, Sicily, nest site selection

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### INTRODUCTION

The occupancy of nest-sites and surrounding areas by raptors is non-random, indicating a preference for certain terrains, apparently of higher quality (Warkentin & James 1988, Sergio & Newton 2003, Espie et al. 2004). Several factors, such as terrain features (elevation, slope, and orientation), competitors, rainfall, and landscape patchiness influence the choice of nesting sites (Ontiveros 1999, Sánchez-Zapata & Calvo 1999, McDonald et al. 2004, Sergio et al. 2004, Rodríguez et al. 2007, Martínez et al. 2008). These constraints define a subset of profitable sites from a larger number of possible nest-sites available every year

for breeding pairs (Ens et al. 1992, Rodenhouse et al. 1997, Sergio & Newton 2003). Site quality may also influence breeding performance especially in raptors showing a strong territory fidelity as predicted by the site-dependent population regulation hypothesis (Newton 1991, Rodenhouse et al. 1997, Franklin et al. 2000, Sergio & Newton 2003, Espie et al. 2004). Thus, it is possible to assess nest-site quality by ranking sites on the basis of frequency of occupancy because territories occupied for longer are more productive (Newton 1991, Rodenhouse et al. 1997).

The European Lanner Falcon subspecies *Falco biarmicus feldeggii* occupies a vast geographical area including Italy, the Balkans, Turkey and the

Caucasus with a patchy distribution (Leonardi 2001). BirdLife International (2004, 2012) estimated that the majority of breeding pairs (480–900) live in Italy and Turkey where they showed a moderate decline ( $> 10\%$ ) in the recent past (1990–2000). In addition, the latest national survey in Italy estimated no more than 140–172 pairs with many small vulnerable demes on the mainland and a large one (70–80 pairs) inhabiting Sicily (Andreotti & Leonardi 2007, Andreotti et al. 2008). The European subspecies nests almost exclusively on rocky cliffs in open and steppe-like habitats, pasturelands, and abandoned fields that are unfortunately not well represented in the protected areas, especially in Sicily (Leonardi 2001, Andreotti et al. 2008). Some comprehensive studies described nest-site characteristics in Sicily (Massa et al. 1991), central Italy (Bassi et al. 1992) and also, at landscape level, in all the Italian breeding range (Andreotti et al. 2008). A similar study was carried out in southern Africa on the subspecies *F. b. biarmicus* (Jenkins 1994). Nevertheless, there is a lack of information on the influence of different territory quality on nest selection and breeding performances of this falcon (Newton 1991, Rodenhouse et al. 1997, Leonardi 2001).

Many studies were focused on competitive relations with the sympatric Peregrine Falcon *Falco peregrinus* (see Jenkins & Hockey 2001 for a review). Although a certain overlap in ecological requirements exists, results confirmed significant differences in nest site selection between these two species (Massa et al. 1991, Jenkins 2000a). On the contrary, it seems that especially in some parts of the Italian mainland, dominant peregrines are in the process of usurping lanner nest-sites (Pellegrini et al. 1994, Martelli & Rigacci 2001, Brunelli pers. com). Also in Sicily, the Lanner Falcon is apparently in competition for nesting cliffs with the local subspecies of the peregrine *F. p. brookei*. Peregrines are widespread in this island, and to some extent they probably affect densities of lanner breeding pairs (Massa et al. 1991, Di Vittorio et al. 2004). Nevertheless as observed in other studies, territorial conflicts are infrequent because peregrines generally select higher cliffs than lanners (Massa et al. 1991, Sergio et al. 2004). Further evidence becomes necessary to evaluate effects of peregrines on nest-sites selected by lanners in the light of different quality nest-sites (high and low; Manzi & Perna 1994).

This research is part of a project aimed at evaluating the effects of different terrain and biocli-

matic factors on breeding populations of the Lanner Falcon in Italy (Andreotti & Leonardi 2007, Andreotti et al. 2008). Firstly, we tried to assess (1) differences in environmental attributes among breeding sites and (2) their consequences on mean productivity. Then, we related site selection by lanner pairs to (1) the occupancy rate, (2) nest-site quality, and (3) differences in environmental attributes of Peregrine nest-sites. Finally, we discuss our results in the light of conservation implications for this rare and localised subspecies.

## METHODS

### Study area

This study was carried out in an area of 4769 km<sup>2</sup> in central and central-eastern Sicily (southern Italy, 37°95'–37°17'N, 12°96'–14°96'E). Geomorphological features consist of flat regions alternated with moderately steep hills ranging from 209–1062 m above sea level. Dominant habitats at lower altitude are pasturelands and extensive monoculture fields, substituted by shrubs and wood remnants at high elevations. Throughout, there are several different orchards, mainly olive yards and citrus groves.

### Monitoring falcon pairs

During four breeding seasons (2003–2006), we found and regularly checked 37 nesting sites occupied at least once by large falcons (both lanners and peregrines). We conducted 114 observational sessions with an average of 4.2 visits per site/season. In addition, we monitored each lanner nest to ascertain the number of young fledged annually. According to Hardey et al. (2006), the nest-site is a scrape on a cliff ledge (eyrie) and its immediate surroundings, whereas the nesting territory is the immediate area around the nest defended by the breeding pair. We identified territorial pairs before nest initiation and we considered a pair successful when at least one young fledged (Hardey et al. 2006). We considered the number of young fledged per successful pair as the most reliable dependent variable for evaluating influences of habitat characteristics on breeding performance (Steenhof & Kochert 1982). Finally, we utilized the proportion of years that a site was occupied by lanner pairs across the study duration as a measure of territory quality because its association with productivity tends to be already apparent in shorter study periods ( $< 4$  years; Sergio & Newton 2003).

### Digital terrain variables

Nest positions were located by GPS devices (IMATE PDA-N) in WGS84 format. Then, the data was re-projected to Gauss Boaga (Monte Mario 2 Italy) in ArcMap 9.3 (ESRI 2008). We considered a circular sample area with a nest-site occupied by lanners or peregrines in its centre and a 3000 m buffer zone around it. Then we subdivided each sample area in square cells (circular area = 2827 ha; perimeter = 18849 m; columns and rows = 5484; cell size  $xy = 83.2 \times 83.2$  m). We obtained nest-site characteristics from the cell on which the nest is placed and nesting territory features as a mean from all cells included in the circular sample area (Table 1). Terrain variables come from the Digital Evaluation Model (DEM) dataset (GTOPO30), originally provided by US Geological Surveys EROS Data Center (Sioux Falls, South Dakota). Grid cells were characterized by four terrain variables: slope, aspect, hillshade, and elevation (Table 1). We calculated the Euclidean distances from waterbodies (rivers, lakes etc.) and protected areas (Special Protection Areas — SPAs, Special Areas of Conservation — SACs) due to their importance as potential food sources. Nevertheless, SPAs, SACs and waterbodies are so far from nest sites and/or covering very small territories (Andreotti et al. 2008). Thus, we decided to avoid their inclusion in the analysis. Climate data were derived from the WorldClim database

(<http://www.worldclim.org>), which is a set of global climate layers (climate grids) with spatial resolution of a square kilometre (Table 1). They are long-term average variables calculated as interpolations of observed data representative of 1950–2000 (Hijmans et al. 2005). The bioclimatic variables represent annual trends (mean temperature — AMT and mean precipitation — AP, Table 1) and extreme or limiting environmental factors (MTWaQ, MTCQ, PWeQ, PCQ etc.; Table 1). Values were divided per period of three months (1/4 of the year or “quarter”) and temperatures are presented in  $^{\circ}\text{C} \times 10$  (Hijmans et al. 2005).

### Statistical analysis

We divided all monitored nest sites ( $n = 37$ ) into two main groups on the basis of which species has bred during the study period (L = Lanner; P = Peregrine). Each site belongs to a species when it was occupied at least once during all four breeding seasons (L = 26; P = 15). In particular, peregrines have used eleven sites exclusively and four more by replacing the Lanner. The occupancy rate was calculated for each nest-site ( $n = 26$ ) as the proportion of years with lanner pairs on the total four years study period ( $n/N$ ).

According with Sergio & Newton (2003), we subdivided Lanner nest-sites using the occupancy rate as the main clue of quality. In fact, the occupancy is a simple measure of habitat quality

Table 1. Variables used to characterize nests and site area occupied by breeding falcon pairs in eastern Sicily. Each sample areas (circular area = 2827 ha) subdivided in square cells ( $xy = 83.2 \times 83.2$  m). Nest-site characteristics obtained from the cell on which the nest is placed and nesting territory features as a mean from all cells included in the circular sample area. Temperatures are in  $^{\circ}\text{C} \times 10$  (Hijmans et al. 2005).

Variables	Description
<b>Nest site characteristics</b>	
NSH	Solar light received (azimuth of the light source $315^{\circ}$ , altitude $45^{\circ}$ )
NS	Slope value of the cell with a nest ( $^{\circ}$ )
NA	Altitude above sea level of the nest (m)
ASP	The compass direction (measured from the north) that a topographic slope faces ( $^{\circ}$ )
<b>Nesting territory characteristics</b>	
NTH	The mean solar light received (azimuth of the light source $315^{\circ}$ , altitude $45^{\circ}$ )
NTS	The mean slope value of the nest area ( $^{\circ}$ )
NTA	The mean altitude above sea level of the nest area (m)
<b>Bioclimatic variables</b>	
AP	Annual precipitation (mm)
AMT	Annual mean temperature (mm)
MTWeQ	Mean temperature of wettest quarter ( $^{\circ}$ )
MTDQ	Mean temperature of driest quarter ( $^{\circ}$ )
MTWaQ	Mean temperature of warmest quarter ( $^{\circ}$ )
MTCQ	Mean temperature of coldest quarter ( $^{\circ}$ )
PWeQ	Precipitation of wettest quarter (mm)
PDQ	Precipitation of driest quarter (mm)
PWaQ	Precipitation of warmest quarter (mm)
PCQ	Precipitation of coldest quarter (mm)

suitable for species in heterogeneous habitats and for populations in which not all territories are occupied every year as the Lanner Falcon (Leonardi 2001, Sergio & Newton 2003). Related to the four years study period, sites may have 0.25 – 0.5 – 0.75 and 1 occupancy rates respectively. Thus, we considered a priori as low occupancy sites those with  $\leq 0.5$  rate values (L2) and  $> 0.5$  as high occupancy ones (L1). Then, we tested differences between terrain and bioclimatic characteristics of L1 and L2 breeding sites using non-parametric Mann–Whitney U test with Monte Carlo permutation test (number of re-samples 10000;  $n = 26$ ). We adopted the same procedure for comparisons between both L1 and L2 sites and sites occupied by peregrines (P;  $n = 15$ ). Finally, we checked for multicollinearity among terrain and bioclimatic variables, then chose a reasonable subset of fewer uncorrelated variables applying sequential likelihood ratio tests (LRTs, Zuur et al. 2009). Thus, we ran a generalised linear model (GLM) with a Poisson response to determine which environmental factors influenced the mean number of fledglings per successful pair. All tests were performed with Statistica 7.0 (Statsoft Inc., 2005).

## RESULTS

### Territory occupancy rate

Lanner pairs occupied 26 breeding sites during 2003–2006 with different occupancy rates (2003 = 19 sites, 2004 = 15, 2005 = 13 and 2006 = 9;  $n = 56$  site \* years). As predicted by the site-dependent population regulation hypothesis, mean number of young fledged per territorial pair was positively related to occupancy rates (one-way ANOVA,  $F = 5.021$ ,  $df = 3, 22$ ;  $p = 0.008$ ; Fig. 1), and successful pairs (one-way ANOVA,  $F = 18.322$ ,  $df = 3, 13$ ;  $p < 0.001$ ). During the four-year study period, a few high quality nest-sites ( $n = 6$ ) raised 58% of young produced in the whole study area ( $n = 74$ ).

### Differences in characteristics of low and high occupancy nest-sites

Occupancy rankings showed significant differences in environmental attributes between L1 and L2 nest sites (Table 2). Such differences were related to the main terrain and bioclimatic determinants, including the nest-site altitude, the mean altitude and the mean temperature of the coldest quarter of nesting territories (Table 2). Among terrain and bioclimatic independent variables,

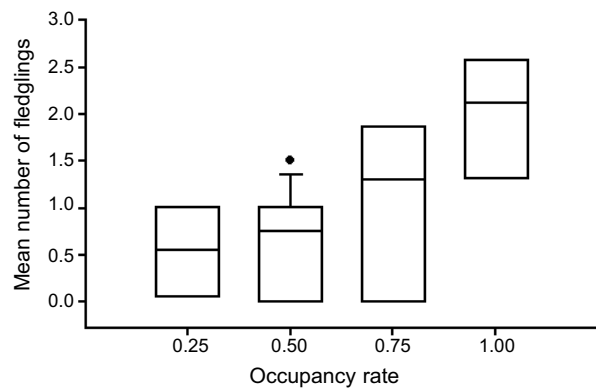


Fig. 1. The relationship between mean number of fledglings per Lanner Falcon territorial pair and occupancy rate of nest-sites in Eastern Sicily. The boundary of the box closest to zero indicates the 25th percentile, the line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers (error bars) above the box indicate the 90th percentiles.

LRTs selected a small subset of uncorrelated variables (NS  $\chi^2 = 4.981$ ; NTS  $\chi^2 = 3.689$ ; MTWeQ  $\chi^2 = 2.162$ ; PCQ  $\chi^2 = 1.2865$ ; ASP  $\chi^2 = 1.185$ ). The generalised linear model revealed a significant effect of the slope of the nest-site (NS) on mean fledgling number per successful pair (Wald statistic = 4.468,  $df = 1$ ,  $p = 0.031$ ).

### Differences with peregrines

The mean slope of the nest territory (NTS) is an important predictor for differentiating the cliff selection of Lanner Falcon and peregrines (L1 and P;  $p = 0.007$ ; Table 2) together with the slope of the nest-site (NS;  $p = 0.015$ ; Table 2) and the mean elevation of the area (NTA;  $p = 0.028$ ; Table 2). On the contrary, slope values of L2 nest-sites and nesting territories showed no significant differences with those of peregrines suggesting a potential overlap (Mann-Whitney U test,  $Z = -1.289$ ,  $n = 24$ ,  $p = 0.202$ ;  $Z = -1.642$ ,  $n = 24$ ,  $p = 0.109$ ).

## DISCUSSION

The occupancy rate of territories by pairs is considered as a reliable indirect measurement of habitat quality, and, typically, a positive relationship has been found between territory rank and breeding performance (Newton 1991, Ens et al. 1992, Espie et al. 2004). Our results confirmed this assumption also for lanners and, as expected, the measured heterogeneity in occupancy was clearly associated with productivity during a short-term

Table 2. Comparisons between characteristics of high (L1) and low (L2) occupancy nest sites of the Lanner Falcon and those of the Peregrine Falcon (P) in eastern Sicily. Data presented as mean  $\pm$  SD. Statistics based on Monte Carlo tests (2-tailed) with 10000 resamplings. Temperatures are in  $^{\circ}\text{C} \times 10$  (Hijmans et al. 2005).

Variables	L1	L2	P	L1 vs L2		L1 vs P	
	n = 12	n = 14	n = 15	Z	p	Z	p
<b>Nest characteristics</b>							
NSH	163.75 $\pm$ 41.33	164.92 $\pm$ 54.58	147.714 $\pm$ 69.733	-0.317	0.764	-0.489	0.644
NS	17.62 $\pm$ 9.43	21.71 $\pm$ 8.76	26.536 $\pm$ 6.414	-0.879	0.388	-2.393	0.015
NA	391.25 $\pm$ 113.28	553.78 $\pm$ 199.78	523.143 $\pm$ 236.062	-2.660	0.006	-1.415	0.169
ASP	177.00 $\pm$ 105.47	221.93 $\pm$ 73.34	184.786 $\pm$ 106.439	-1.196	0.238	-0.026	0.992
<b>Nesting territory characteristics</b>							
NTH	173.58 $\pm$ 5.38	176.27 $\pm$ 3.84	170.929 $\pm$ 12.054	-1.954	0.053	-1.082	0.287
NTS	8.05 $\pm$ 1.77	8.76 $\pm$ 1.71	10.118 $\pm$ 1.705	-1.197	0.238	-2.599	0.007
NTA	331.16 $\pm$ 109.75	468.00 $\pm$ 195.56	496.786 $\pm$ 208.860	-2.099	0.037	-2.186	0.028
<b>Bioclimatic variables</b>							
AP	60.58 $\pm$ 4.88	61.14 $\pm$ 3.71	61.400 $\pm$ 3.942	-0.344	0.747	-0.221	0.843
AMT	178.17 $\pm$ 3.51	174.21 $\pm$ 5.64	174.667 $\pm$ 5.912	-1.867	0.067	-1.643	0.102
MTWeQ	118.08 $\pm$ 5.28	112.28 $\pm$ 8.42	113.000 $\pm$ 8.660	-1.937	0.053	-1.640	0.103
MTDQ	209.50 $\pm$ 2.07	207.43 $\pm$ 2.90	207.533 $\pm$ 3.067	-1.576	0.117	-1.780	0.081
MTWaQ	157.83 $\pm$ 4.11	153.57 $\pm$ 6.03	153.733 $\pm$ 6.170	-1.671	0.095	-1.917	0.054
MTCQ	186.50 $\pm$ 3.11	183.07 $\pm$ 4.85	183.600 $\pm$ 5.026	-2.099	0.033	-1.526	0.135
PWeQ	61.00 $\pm$ 4.22	60.28 $\pm$ 3.31	62.067 $\pm$ 4.079	-0.491	0.638	-0.612	0.554
PDQ	24.75 $\pm$ 4.24	26.28 $\pm$ 4.87	26.533 $\pm$ 5.680	-0.908	0.370	-0.320	0.763
PWaQ	23.92 $\pm$ 2.81	21.71 $\pm$ 4.33	22.733 $\pm$ 3.262	-1.406	0.171	-1.157	0.257
PCQ	80.75 $\pm$ 10.69	81.92 $\pm$ 6.86	79.933 $\pm$ 9.161	-0.195	0.858	-0.440	0.681

study period (Sergio & Newton 2002). Generally, an overestimation of the number of actual nesting pairs is possible due to the presence of sites with low occupancy rates (Fig. 1; Ferrer & Donázar 1996; Krüger & Lindström 2001, Sergio & Newton 2002). According with Sarà (2008), this low fidelity to low quality sites by the lanners may confound repeated surveys on a large regional scale and population abundance modelling. For instance, a pair changing its nest-site may be counted several times in subsequent breeding seasons leading to an overestimate of the population. In fact, more than 120 pairs were predicted in Sicily by the Regional Atlas, but our results according with Sarà (2008) suggest a smaller effective breeding population size (probably 70–80 pairs — Andreotti & Leonardi 2007).

Preliminary unpublished observations revealed high failure rates ranging from 22 to 40% (own data). A long-term investigation on Merlins *Falco columbarius* provided evidence that bird quality, and to a lesser extent nest-site quality, influences reproduction in a natural population (Espie et al. 2004). A recent study, made upon the same breeding population of lanners, revealed a significant relationships among productivity and vocal activities, an indirect measure of quality of male partners (Leonardi et al. 2013). Thus, our results reinforce the idea that both internal and external

factors likely act in combination to constrain breeding performance (Espie et al. 2004).

Different studies on aspect of cliffs used by raptors revealed a trend toward southward orientations (Ontiveros 1999, Sullivan et al. 2003, Brambilla et al. 2006). Both high and low quality lanner sites were mainly southward oriented according to previous observations (Table 2, Bassi et al. 1992, see Leonardi 2001 for a review). Nevertheless, this study suggests that the aspect of cliffs as well the “hillshade” which measures the solar light received in the cell with the eyrie have no influence on lanner mean productivity. Several authors reported negative effects of rainfall on territory occupancy, breeding frequency and breeding success of the Peregrine and the Brown Falcons *Falco berigora* (Olsen & Olsen 1989, Jenkins 2000a, McDonald et al. 2004). According with Carrilo & Gonzales-Davila (2010) in our model rainfall frequency was not a good predictor of fledging success in semi-arid environments.

Previous studies reported the preference by the lanner for low cliffs as nesting sites (Massa et al. 1991, Bassi et al. 1992, Jenkins 1994, Manzi & Perna 1994). Manzi & Perna (1994) considered low cliffs used by lanners as poor quality sites compared to those occupied by peregrines in the same area (Marches, central Italy). Conversely, Jenkins (1995) suggested that lanners are residents of low

relief areas because they are efficient users of thermals which support active search hunting techniques that ultimately improve provisioning rates at nests (Jenkins 1992). As in our study population, fledging rates varied significantly between sites in the Soutpansberg (South Africa) assuming different quality ranks (Jenkins 2000a). Our results are coherent with those on South African lanners (Table 2). In addition, high quality nest-sites seem to play a key role on population viability (Penteriani et al. 2004).

Generally, peregrine nesting sites were settled on higher and steeper cliffs in relation to their availability in the territory (Jenkins 2000b, Sergio et al. 2004, Brambilla et al. 2006, Rodríguez et al. 2007). Probably, the vertical height improves the chance of a successful hunt of a perch-hunting predator such as the peregrine (Jenkins 2000b). In eastern Sicily this falcon showed similar preferences, with the slope of the eyrie and the mean inclination of the surrounding reliefs the most important predictors of its presence (Table 2; Brambilla et al. 2006). Although a certain overlap for nesting sites exists, both falcon species have different selection preferences (Table 2; Jenkins 2000a, Jenkins & Hockey 2001). Overall, turnover between the two falcons has been recorded in Sicily and in several regions of the Italian peninsula (Di Vittorio et al. 2004, Andreotti & Leonardi 2007, Brunelli pers. com). In addition, Sarà (2008) suggested that the competition with the peregrine might constrain the lanner's potential abundance in Sicily. In our study area, we supposed that peregrine dominance regards mainly low quality sites where lanners have low occupancy rates and fewer young fledged per year. The turnover becomes evident in these nest-sites deserted by lanner pairs with terrain feature suitable for the peregrine.

The Lanner Falcon breeding population in Sicily represents a significant part of the whole population in the Western Palearctic (Leonardi 2001). Thus, the viability of this population is crucial for preserving a good genetic pool of this subspecies. Our results indicated (1) the different quality of nest-sites and (2) the key role of the few high quality sites, which contribute a large proportion of fledglings to our study area. Thus in our opinion, it is a conservation priority to develop a predictive model that allows identification of both low and high quality sites in the entire Sicilian territory. By this way, it should be possible (1) to preserve the annual production of young of the best territories, (2) to assess the total number

of suitable breeding sites, and (3) to evaluate the effective contribution of the low quality sites for the persistence of a viable population in Sicily.

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## STRESZCZENIE

**[Wpływ czynników środowiskowych i jakości miejsca lęgowego na liczbę podlotów u raroga górskiego]**

Badania prowadzono na Sycylii w latach 2003–2006. Wyszukano i regularnie monitorowano 37 miejsc gniazdowych zajętych przynajmniej jeden raz przez raroga górskiego i/lub sokoła wędrownego. Określano liczbę podlotów, oraz zmienne środowiskowe i klimatyczne dla gniazda i terytorium wokół niego (Tab. 1). Wydzielono dwie kategorie miejsc gniazdowych w zależności od liczby sezonów, przez które były one zajęte przez rarogi: L1 — o częstym (ponad dwa sezony) i L2 — rzadkim (do dwóch sezonów) wykorzystaniu.

Miejsca lęgowe różniące się częstością wykorzystania przez rarogi różniły się kilkoma zmiennymi środowiskowymi, w tym wysokością n.p.m. (Tab. 2). W porównaniu do miejsc gniazdowych sokoła wędrownego (który może przejmować miejsca wykorzystywane przez rarogi), często zajmowane miejsca gniazdowe rarogów znajdowały się na niższych i mniej stromych skałach (Tab. 2).

Stwierdzono, że im częściej zajmowane jest dane miejsce lęgowe, tym większa liczba piskląt jest z niego wyprowadzana (Fig. 1). Na liczbę podlotów wpływało także nachylenie terenu w najbliższej okolicy gniazda. W ciągu 4 lat badań z 6 najczęściej wykorzystywanych miejsc gniazdowych zostało wyprowadzonych 58% wszystkich zaobserwowanych w tym czasie piskląt.