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Spatial patterns of territorial large falcons influence mixed pair formation in an arid environment

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Abstract Interspecific crossbreeding among breeding populations can lead to outbreeding depression and reduce individual fitness. Mixed pairs occur more frequently in areas with fragmented habitat where individual species often have low population densities. Due to the genetic affinities among falcons, hybrids from within this group exhibit full or partial fertility, presumably over indefinite generations. This study aims to ascertain the influence of spatial patterns of territory holders (pairs and non-paired individuals) on the occurrence of mixed pairs among large falcons (Barbary *Falco peregrinus pelegrinoides* and Lanner Falcons *F. biarmicus tanypterus*) in Saudi Arabia. We found that mixed pairs occurred in study areas (5.4% of territories) with higher nearest neighbour distances (NND). Densities per se had no effect on the occurrence of mixed pairs, and neither did the quality of territories. Favourable but restricted core areas maintain a healthy breeding population but separated by very large unfavourable terrains. Distances from core areas affect the presence of pairs and unpaired falcons. Higher distances (>200 km) force potential breeders to mate and breed interspecifically. Probably a modest risk of outbreeding depression occurred, but the desirable re-establishment of gene flow between population fragments, also using reintroduction techniques will minimize the risk by decreasing the chance for the occurrence of mixed pairs.

Keywords: *Falco biarmicus tanypterus*, *Falco peregrinus pelegrinoides*, hybridization, Saudi Arabia

Összefoglalás Az egyes fészkelőfajok állományainak kereszteződése „outbreeding depression” -hez vezethet, ami végső soron csökkenti az egyedi fitneszt. Eltérő fajokhoz tartozó párok gyakrabban fordulnak elő fragmentált élőhelyeken, ahol az egyes fajok állománysűrűsége alacsony. Genetikai közelségük miatt a sólyomfajok közötti hibridek teljes vagy részleges termékenységet mutatnak, feltehetően végtelen számú generáción át. Jelen vizsgálat célja a foglalt revírek (párok és egyedül foglaló példányok) területi mintázatának a kevert, nagytestű sólyom (sivatagi sólyom *Falco peregrinus pelegrinoides* és Feldegg-sólyom *F. biarmicus tanypterus*) párok előfordulására gyakorolt hatását törekszik bemutatni szaúd-arábiai adatok alapján. Azt találtuk, hogy a kevert párok (a revírek 5,4%-a) a vizsgált területen belül ott fordultak elő, ahol a legközelebbi szomszédok nagyobb távolságra voltak (nearest neighbor distance, NND). Az állománysűrűségnek közvetlenül nem volt hatása a kevert párok előfordulására, ahogy a revírek minőségének sem. Az előnyben részesített, de korlátozott kiterjedésű magterületek egészséges fészkelőállománynak adtak otthont, azonban ezek nagy kiterjedésű, a sólymok számára alkalmatlan területekkel voltak elválasztva. A magterületektől való távolság meghatározza a párok és a pár nélküli, revírt foglaló madarak jelenlétét. A nagyobb távolság (>200 km) pedig arra kényszeríti az ivarérett madarakat, hogy más fajjal álljanak párba és kezdjenek költésbe. Az outbreeding depression megjelenésének feltehetően van némi esélye, de a töredékállományok közötti génáramlás helyreállítása, akár visszatelepítési technikák alkalmazásával is, mérsékelni fogja ezt a kockázatot, csökkentve a valószínűségét a kevert párok megjelenésének.

Kulcsszavak: *Falco biarmicus tanypterus, Falco peregrinus pelegrinoides*, hibridizáció, Szaúd-Arábia

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Introduction

Interspecific crossbreeding may be an evolutionary mechanism that allows increased genetic diversity and can be a relatively common phenomenon in some avian sister taxa (Pierotti & Annett 1993, Randler 2006, Gholamhosseini *et al.* 2013). Genetic differences among partners can lead to outbreeding depression, and consequently, to a reduction of their breeding fitness (Frankham *et al.* 2011, Ralls *et al.* 2013). The establishment of mixed pairs within avian genera occurs more frequently in areas with fragmented habitat and/or at the border of two species' ranges (Panov 1989, Harrison 1991, Pierotti & Annett 1993). In these marginal zones, ecologically distinct forms often have low population densities, and they are more prone to genetic erosion (Barton & Hewitt 1985, Frankham *et al.* 2011). Thus, lack of conspecific forces potential breeders to mate and breed interspecifically (Wilson & Hedrick 1982, McCarthy 2006). Usually, reproductive isolation mechanisms and behavioural barriers should prevent interbreeding between species potentially resulting in outbreeding depression (Angelov *et al.* 2006, Gjershaug *et al.* 2006).

Several records of mixed pairs and hybridization events regarding raptors in the wild (Panov 1998, Gjershaug *et al.* 2006, Cugnasse *et al.* 2017, Literák *et al.* 2019). Due to the genetic affinities among falcons (genus *Falco*), hybrids from within this group exhibit full or partial fertility, presumably over indefinite generations (Heidenreich *et al.* 1993, Nittinger *et al.* 2005, McCarthy 2006). In fact, evolutionarily they are a rather young species with a high propensity to hybridize (Prager & Wilson 1975, Nittinger *et al.* 2005). There are reports about interbreeding among mixed pairs of Saker *(F. cherrug)* and Barbary Falcons *(F. p. pelegrinoides)*, Peregrine *(F. peregrinus)* and Gyrfalcons *(F. rusticolus)*, Saker and Lanner Falcons *(F. biarmicus)*, as well with all hybrids escaped from falconry (Boev & Dimitrov 1995, Gjershaug *et al.* 2006, Everitt & Franklin 2009, Dixon 2012, Cugnasse *et al.* 2017). The *Hierofalco* sub-genus (Saker, Gyr- and Lanner Falcons) indicate a very low genetic distance (>2%) but crossing with Peregrine Falcons usually produce sterile female offspring (Pomichal *et al.* 2014). Overall, genetic introgression to local falcon populations and the relative presence of hybrids are the main effects of direct and indirectly human activities (Fleming *et al.* 2011, Dixon 2012).

The Barbary Falcon *(F. p. pelegrinoides)* is a subspecies of the Peregrine Falcon inhabiting a vast geographical area from the Canary Islands to the Arabian Peninsula including all North African countries (Brosset 1986, White *et al.* 2013, Rodríguez *et al.* 2019). Interbreeding occurs among Barbary Falcons and other Peregrine subspecies (i.e. *F. p. brookei*) but rarely with *hierofalcons* such as Saker and Lanner Falcons (Brosset 1986, Angelov *et al.*

2006, McCarthy 2006, Rodríguez *et al*. 2019). For the latter species although its breeding range largely overlaps with Barbary Falcons, interspecific crossbreeding records have only occurred among captive birds (McCarthy 2006). The Lanner Falcon could be in competition for nest sites with the Barbary Falcon in several areas in North Africa and the Middle East (Leonardi 2015). Overall, habitat segregation separates these large falcons with the Barbary Falcon as the dominant species, probably due to its use of safe high cliffs avoided by the Lanner Falcon (Ledant *et al.* 1981, Amato *et al.* 2014, Binothman 2016). Thus, it is reasonable that habitat requirements and behavioural patterns (i.e. dietary difference) can limit mixed-species pairings between the two species (Gjershaug *et al.* 2006).

The main aim of this study was to ascertain the influence of spatial patterns of territory holders (pairs and non-paired individuals) on the occurrence of mixed pairs among large falcons in Saudi Arabia. Results are discussed in terms of the potential conservation implications for these threatened species.

Methods

In Saudi Arabia, intensive field studies in the whole country have been conducted since 2015 to investigate 1,255 putative Lanner and Barbary Falcons nest sites (Binothman 2016). Preliminary analyses indicate a low rate of active Barbary Falcon nests (>15%, n = 725), with unpaired males occupying 4% of inactive nests (Binothman 2016).

In-depth field surveys were conducted in three sample areas identified across the breeding range of the Barbary Falcon in Western and Central Saudi Arabia in 2021 *(Figure 1)*. The first area (A – 158,125 km^2, perimeter = 1,953 km) was within the Medina province, the second (B – 128,771 km^2, perimeter = 1,403 km) in the Riyadh region (Central Arabia) and the third (C – 70,907 km^2, perimeter = 1,285 km) across Al-Bahah/’Asir provinces. Sample area A is characterized by a cold-dry climate with a desert subzone, area B is a hot-dry desert subzone and area C is a subtropical and Mediterranean subzone (Alrasheda & Asif 2015). For the statistical analysis, sample areas were grouped based on the presence (MIX) or absence (ABS) of mixed pairs. In the early part of the breeding season, each nesting site was categorized based on presence of a pair or an un-paired territory holder.

Barbary Falcon nest locations were plotted on a map using QGIS software (ver. 3.14). Nearest neighbour distances (NND) for all located Barbary Falcon nests were measured on the map from centre of an occupied territory to the centre of the nearest neighbour’s territory (Solonen 1993, Martínez-Hesterkamp *et al.* 2018). Following Brown (1975), the regularity of nest spacing (G-statistic) was calculated as the ratio between geometric and arithmetic means of the squared nearest-neighbour distances. Values ranged from 0 to 1 with those >0.65 indicating a regular dispersion of nest sites and those close to 0 randomness (Brown 1975). The Clark and Evans (1954) aggregation index (R) was used to assess whether the spatial distribution of nests differed significantly from the null hypothesis of complete spatial randomness. A value of R =1.0 represents randomness, R >1.0 regularity and R <1.0 aggregation (Clark & Evans 1954). Nevertheless, the exact null distribution for randomly dispersed points depends upon the geometry of the studied population (areas

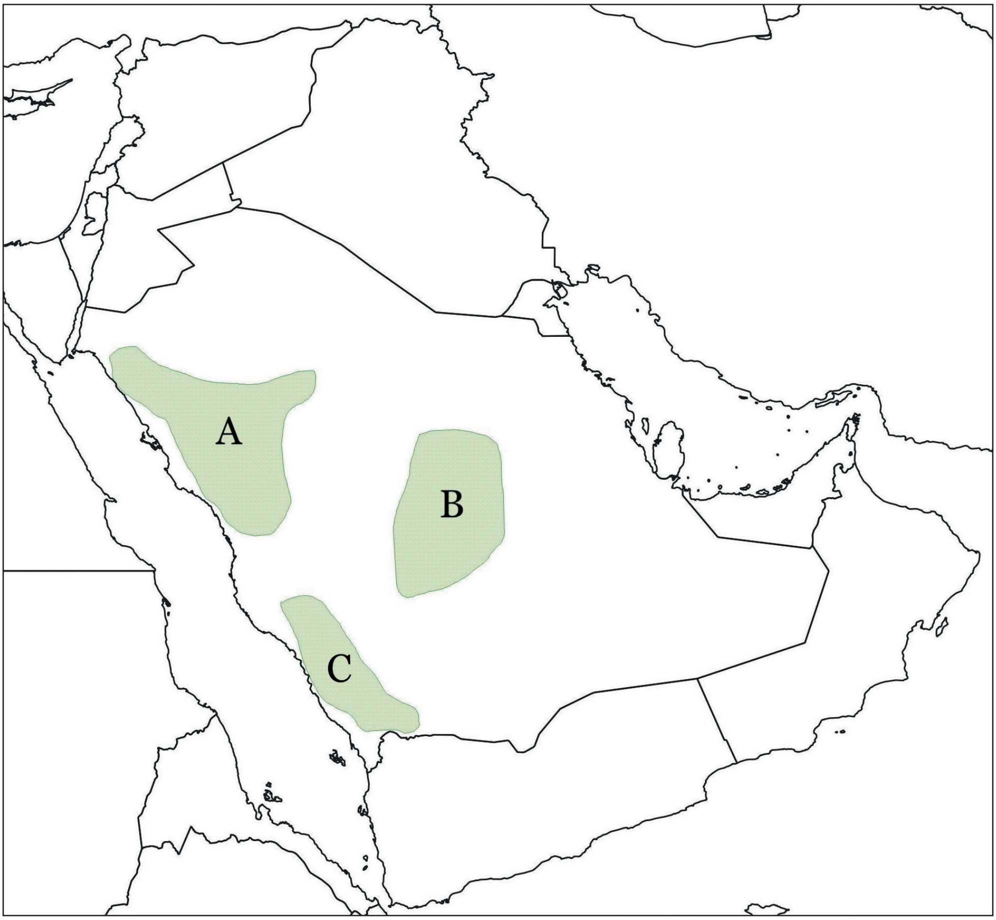

Figure 1. Map showing the three study areas for the Barbary Falcons: Medina province (A), Riyadh region (B), and in Al-Bahah and Asir provinces (C) of Saudi Arabia

1. ábra Térkép a sivatagi sólyom kutatásának három mintaterületéről: Medina tartomány (A), Rijád régió (B), valamint Al-Bahah és Asir tartományok (C) Szaúd-Arábiában

and perimeters) (Connor & Bowers 1987). Thus, as suggested by Donnelly (1978) a modification for bias was made following the mathematical procedure in Krebs (1989). In addition, this correction become necessary when working with small sample sizes (n = <100) as in the present study (Donnelly 1978, Krebs 1999). As suggested by Morandini *et al.* (2020), the average number of fledglings in each territory was used as surrogate of territory quality.

A one-way analysis of variance (ANOVA) was used to analyse differences in the mean-nearest distances between the MIX and ABS groups, while the Kruskal-Wallis test was applied to assess differences in the number of fledged chicks between the same groups (Sokal & Rohlf, 1981). Median densities were compared between groups by means of Mann-Whitney U-tests (Siegel & Castellan 1988). Statistical analyses were performed using SPSS 21.0 (IBM Corp., Armonk, NY) and significance was set at $P < 0.05$.

Table 1. Mean nearest neighbour distances (NND) in km, and observed *G* values for the two study groups (with (M), and without (A) mixed pairs). The probability (P) that the G value was larger than expected from a random distribution was calculated using Clark and Evans (1954) aggregation index (R) modified by Krebs (1989)

1. táblázat Az átlagos legközelebbi szomszéd távolság (nearest neighbor distance, NND) kilométerben, és a G érték a két vizsgált csoportra (M – kevert pár, A – nem kevert pár). A valószínűség (P), hogy G értéke magasabb lesz a véletlenszerű eloszlásból számított értéknél, Clark és Evans (1954) aggregációs R-indexe alapján került kiszámításra, Krebs (1989) által módosított formulával

Study group	**Occupied territories/ 100 km² (*n*)**	**Un-paired falcons (*n/N*)**	**Productivity**	**NND (km)**	*G*	*R*	*z*	*p*
MIX	0.007 (21)	0.82	1.92	284.8±158.8	0.59	4.87	25.5	<0.001
ABS	0.020 (14)	0.57	2.45	131.5±84.7	0.41	3.54	14.4	<0.001

Results

No active nests of the Lanner Falcon were located during the entire duration of the preliminary survey (2015–2020) and the in-depth survey of 2021 (n=530). In 2021, from 72 checked nest sites of Barbary Falcons in the three study areas, only 35 (ca. 50%) were occupied (A=16, B=7, C=13).

Two mixed pairs, both composed of a Lanner female and Barbary Falcon male, were found in A and B sample areas, respectively. This is the first time that mixed pairs among these two species were reported in the wild. Overall, they represent 5.4% of all occupied territories by Barbary Falcons (n=35). The mixed nest in sample area B was unsuccessful whereas two chicks were raised by the mixed pair in sample area A. Nevertheless, only one fledged from this nest and it was then captured.

The percentage of unpaired territory holders was ca. 71% and they were all males (n=35) *(Table 1)*. Nevertheless, mean densities did not vary between the two (MIX and ABS) study groups Mann-Whitney U-test, n=2, z=−1.225, P=0.221) as well productivity (Kruskal-Wallis test, H=1.672, df=1, P=0.196, n=33). Site dispersion showed a non-regular distribution in both study groups, especially for sample areas without mixed pairs (G=0.41) *(Table 1)*. Nevertheless, the spacing pattern deviated significantly from random toward regularity in both study groups *(Table 1)*. Mixed pairs occurred in study areas with higher NNDs *(Table 1, Figure 2)*. Distances between territories occupied by unpaired falcons and pairs ($F_{1,88}$ =36.164, P=0.0001) and between them ($F_{1,102}$ =11.465, P=0.001) were significantly different among study groups.

Discussion

Results support the hypothesis that spatial patterns of nesting sites have a fundamental role on the occurrence of mixed pairs among Barbary and Lanner Falcons in these arid environments *(Figure 2)*. Overall, the Lanner Falcon could be in competition with the Barbary Falcon in

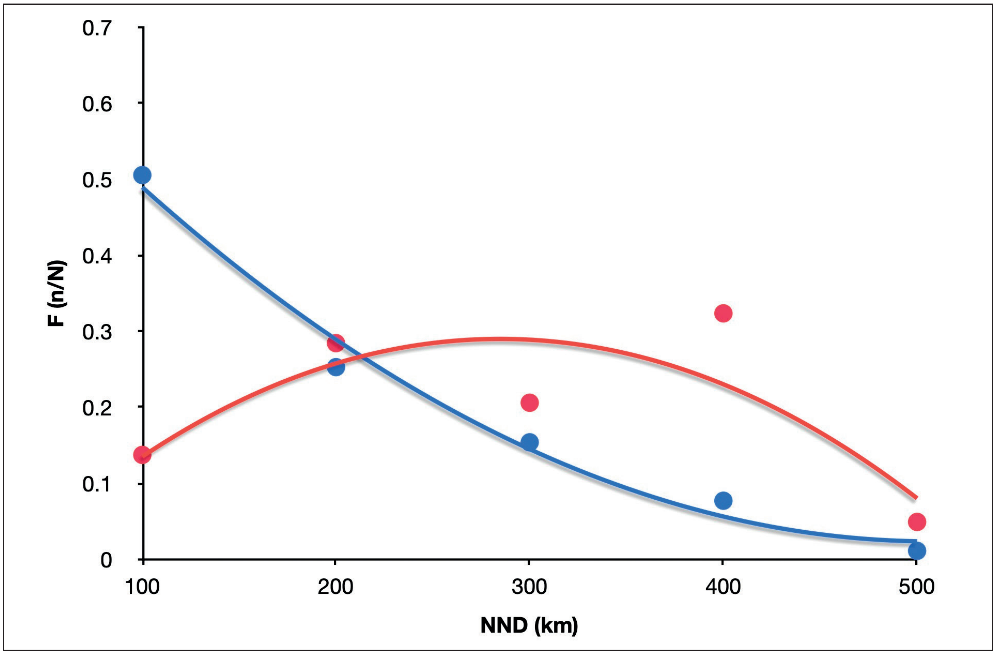

Figure 2. Frequencies of NNDs among study groups consisting of n pairs (n=210) with absence (blue line) or presence (red line) of mixed pairs. Mean NNDs did vary significantly ($F_{1,210}$ =64.301, P=0.0001). Values have been fitted to a second-degree polynomial function

2. ábra Az NND gyakorisága az összes n párból (n=210) álló vizsgált csoportokban, a vegyes párok nélkül (kék vonal) és a vegyes párokkal (piros vonal). Az átlagos NND szignifikánsan változott ($F_{1,210}$= 64,301, P=00001). Az értékekhez egy másodfokú polinomfüggvény lett illesztve

several areas in North Africa and the Middle East (Leonardi 2015). Historical observations in NW Algeria reported a ratio of 3:1 breeding pairs among Barbary and Lanner Falcons (Ledant *et al.* 1981). Unfortunately, no comparative data exists about this possible interaction also in relation species-specific abilities to cope limiting factors other than nest site availability (i.e. food shortage, human pressures). In Saudi Arabia, it is possible that habitat segregation separates these large falcons, but nest sites of both species could be established also at short distance apart (Brosset 1986, Leonardi 2015, Binothman 2016).

Unfortunately, there are few papers devoted to Barbary Falcon breeding biology and even those focus on the Canary Island and North African populations (see White *et al.* 2013 for a review). Although observed NNDs for the Barbary Falcon in Saudi Arabia were significantly higher than in Canary Islands, they correspond to those observed in similar open habitats in Iran (Rodríguez *et al.* 2007, Shafaeipour *et al.* 2016). Study areas without mixed pairs shows an aggregation of territories with NNDs range of ≤100 km and a decrease in numbers at increasing distances *(Figure 2)*. On the contrary, distances in study areas with mixed pairs were higher with a peak of frequency at 300 km far from the core area *(Figure 2)*. The non-regular dispersion of breeding territories deviated from randomness toward regularity in both study groups and was similar to that observed in the Canary Island population (G=0.52) *(Table 1)* (Rodríguez *et al.* 2007).

Although both studied groups include a large number of unpaired territory holders, effects of densities *per se* are negligible as well as the quality of territories *(Table 1)*. These results suggest that favourable but restricted core areas maintain a healthy breeding population but are separated by very large unfavourable terrains. In fact, habitat fragmentation can create a system of discrete patches, inhabited or uninhabited by the local population (Fahrig 2003). Furthermore, habitat fragmentation may significantly impact the number of floated falcons in a meta-population (Lenda *et al.* 2012). In the ABS group, un-paired falcons presumably remain close to the area and wait until a breeding vacancy becomes available (Hunt 1998, Kenward *et al.* 2000). Ultimately, distances from core areas affects the presence of pairs and un-paired falcons but not favour mixed pair formation *(Figure 2)*. Inversely in the MIX group, there is not a core area within 100 km of distance but the whole population (pairs and un-paired falcons) is sparsely spaced by higher distances (>200 km) *(Figure 2)*. Accordingly, un-paired falcons in the study group MIX were far from established breeding pairs but also from other potential partners. Thus, the lack of close conspecific neighbours could force potential breeders to mate and breed interspecifically (Wilson & Hedrick 1982, McCarthy 2006).

The percentage of un-paired Barbary Falcons found inside the three sample areas (A=80%, n=16; B=83%, n=7; C=57%, n=13) is according with 30–70% range reported in comprehensive reviews on raptor populations (Newton 1998, Kenward *et al.* 2000). These territorial males not only increase the intraspecific competition but can try to seduce paired females (Lenda *et al*. 2012). In the MIX group with fewer breeding pairs, poor quality habitats and far from better core areas, males can exhibit an active (non-random) and forced choice towards co-genre female partners.

Overall, the presence and mobility of un-paired falcons should play a crucial role in metapopulation persistence and may constitute a ‘buffer zone’ against population size changes (Lenda *et al.* 2012). In fact, the higher mobility of floaters impact on recruitment rates, the pattern of patch occupancy, and movement between habitat patches (Lenda *et al.* 2012). Nevertheless, in this case of restricted available habitat with a large proportion of un-paired falcons, the higher competition for territories may also increase the probability of local extinction (Penteriani *et al.* 2011, Lenda *et al.* 2012). The occurrence of mixed pairs should be a sign of the same problem but in populations inhabiting unfavourable and fragmented habitats. For genetical different breeding populations such as in our study, the decision tree developed by Frankham *et al.* (2011) suggest a modest risk of outbreeding depression where F_1 individuals are sterile or have very low fitness. Nevertheless, the re-establishment of the gene flow between population fragments is desirable, also by using reintroduction techniques.

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