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ORIGINAL ARTICLE

Parental genetic characteristics and hatching success in a recovering population of Lesser Kestrels

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Abstract Decreased hatchability is a common consequence of inbreeding in oviparous organisms and it has been generally considered a useful measure of the effects of reduced genetic diversity on embryological development. Here, we examined the pattern of hatching failure in a wild population of the endangered Lesser Kestrel (*Falco naumanni*). Particularly, we first analyzed long-term changes of hatching failure over a 16-year study period (1991–2006), in which the study population experienced a concurrent demographic and genetic recovery, and then we determined the consequences of parental genetic characteristics on hatching success. Long-term data analyses revealed a significant decline of hatching failure over time, with annual average hatching failure decreasing from rates characterizing species that have passed a severe population bottleneck to levels generally reported for outbred bird populations. Partial purging of deleterious recessive alleles after the species population decline, the increase of heterozygosity over time reported in a previous study and/or the selection for efficient mechanisms of inbreeding avoidance could be responsible of the observed temporal pattern. In contrast to previous studies, we found no effect of parental genetic characteristics on hatching success. Even though we analyzed an extensive dataset, the 11 neutral markers typed may have had low power to detect such an association. Further, this analysis was limited to the last 5 years (2002–2006) of the whole study period, when DNA samples for genetic analyses were available. During these years, hatching rates were like those typically reported for non-inbred populations, suggesting that the absence of association could be explained by a reduction of the genetic load or consequence of the genetic recover reported in the study population in recent years.

Keywords Genetic diversity · Hatching failure · Heterozygosity · Microsatellite · Relatedness

Introduction

Crosses between genetically related individuals reduce offspring heterozygosity at many genes throughout the genome, resulting in reduced viability and lower physiological efficiency due to the expression of deleterious or partly deleterious recessive alleles and loss of overdominance at some loci (Wright 1977; Charlesworth and Charlesworth 1987). This phenomenon, known as inbreeding depression, can have important consequences on population dynamics and contribute to the decline and eventual extinction of small and isolated natural populations (Saccheri et al. 1998; Westemeier et al. 1998; Madsen et al. 1999). One of the best-established costs of inbreeding is a reduction of fitness early in development (Keller and Waller 2002; Kruuk et al. 2002; Briskie and Mackintosh 2004; Cordero et al. 2004). There are several reasons why the impact of inbreeding depression is expected to be particularly intense during early life stages. First, major genes (i.e., with large effects) are likely to be expressed mainly

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early on during development, so that severer inbreeding consequences are usually manifested in early fitness-related traits (Crawford 1990; Keller and Waller 2002). Second, traits associated with early fitness, such as embryo mortality and offspring survival, are generally subjected to strong natural selection, and thus inbreeding depression is greater for life-history traits closely associated to fitness than for those under weaker selection (De Rose and Roff 1999). Third, selection at early life-stages is likely to reduce variation in inbreeding, hence masking relationships between inbreeding and fitness components later in life (Keller and Waller 2002; Hansson 2004).

Hatching success has been traditionally considered as an informative measure for the study of the consequences of inbreeding and reduced genetic diversity in birds (Westemeier et al. 1998; Briskie and Mackintosh 2004) and oviparous organisms in general (Saccheri et al. 1998). Several studies have found that parental relatedness, estimated either from pedigree data (Greenwood et al. 1978; Van Noordwijk and Scharloo 1981; McRae 1996; Daniels and Walters 2000; Kruuk et al. 2002; Swinnerton et al. 2004; but see Gibbs and Grant 1989; Keller 1998; Jamieson et al. 2003) or using genotypic information (Bensch et al. 1994; Kempenaers et al. 1996; Van de Casteele et al. 2003; Cordero et al. 2004; Hansson 2004; Barber et al. 2005; but see Schmoll et al. 2005; Edly-Wright et al. 2007), reduces hatching success within bird populations. Pedigree-based breeding experiments in poultry research have also provided strong evidence of increased hatching failure in inbred lines (Sittmann et al. 1966). Further, comparative studies have found that hatching success decreases with genetic similarity (Spottiswoode and Møller 2004) and severity of population bottleneck (Briskie and Mackintosh 2004) across species.

The Lesser Kestrel (*Falco naumanni*) is a small-sized colonial and migratory falcon. This species was once one of the most abundant birds of prey in Europe. However, in the middle of the twentieth century it suffered a sharp population decline in its Western Palearctic breeding range that led to a complete extinction in several countries and to strong declines in others (Biber 1990). The Spanish population also experienced a severe population crash, as it dropped from an estimated 100,000 pairs in the 1960s to 4,000–5,000 breeding pairs in the late 1980s (González and Merino 1990). A consequence of this population decline could be a lost of genetic diversity and a concomitant increase of the expression of deleterious recessives (Groombridge et al. 2000; Aguilar et al. 2004) that may have reduced hatching success (Briskie and Mackintosh 2004) and other components of fitness (Ortego et al. 2007a, b).

In the present study, we use data from a long-term population study in combination with estimates of parental relatedness to study the patterns of hatching success in a wild Lesser Kestrel population from Central Spain experiencing a concurrent genetic and a demographic recovery (Ortego et al. 2007c). Particularly, we first analyzed long-term changes of hatching failure over a 16-year study period (1991–2006) and then we determined the consequences of parental genetic characteristics on hatching success. For this last purpose, we used 11 highly polymorphic microsatellite loci that allowed us to estimate the genetic diversity of the father, the mother, and their offspring (predicted based on parental genotype data) to test their influence on zygote viability after controlling for potential non-genetic confounding factors.

Methods

Study population and field procedures

The study was conducted in La Mancha, central Spain (600–800 m above sea level), in an area covering approximately 1,000 km^2 (see Ortego et al. 2007a for a detailed description). We studied 30 Lesser Kestrel colonies clustered in two subpopulations separated by 30 km: the Villacañas subpopulation (39°30′N, 3°20′W; 24 colonies) and the Consuegra subpopulation (39°35′N, 3°40′W; 6 colonies). However, in spite of the low exchange of individuals between both subpopulations, a preliminary analysis showed an absence of structure (Ortego et al. 2007a).

In our study area, Lesser Kestrels form colonies of between 1 and 60 pairs located in abandoned farm houses where they nest under tiled roofs and inside holes in walls (Aparicio 1997). The species is highly philopatric, and most surviving adults, and a third of young return to the same colony to breed (J.M. Aparicio, unpublished data). Egg laying lasts from the end of April to the first week of June (Aparicio and Bonal 2002). They are mainly monogamous, with very low rates of extrapair paternity (Negro et al. 1996; J. Ortego, unpublished data), and lay a single clutch per season (modal clutch size in our population = 4 eggs; range = 1–6 eggs) with the exception of some rare clutches of replacement (ca. 0.5%) that were excluded from this study (Ortego et al. 2007a). Both sexes contribute to incubation, but only females incubate at night (Serrano et al. 2005). During 13 breeding seasons (1991–1994, 1997, 1999–2006), we located nest-sites before the onset of egg-laying. Each potential nest was monitored every 6 days from the middle of April to find the first eggs, and then every 2 days until the clutch was finished. Thus, since females usually lay four or five eggs with mean intervals of 2 days, we were able to find the maximum number of unfinished clutches with the minimum disturbance of the colonies. Laying date was defined as the date the first egg was laid (Aparicio and Bonal 2002). Near expected hatching dates, we inspected the nests regularly to ascertain the exact hatching pattern of the eggs. We defined as unhatched eggs those that survived the entire incubation period but failed to hatch (Serrano et al. 2005). Clutches that had disappeared or had been lost due to predation or abandoned were excluded from the dataset.

During the 2002–2006 breeding seasons, we carried a more intensive monitoring of the population. During these breeding seasons, we trapped adults with a noose carpet or by hand during incubation, and measured and individually marked them with metallic and coloured plastic rings. Blood samples (100 μl) were obtained by venipuncture of the brachial vein and preserved in ~1,200 μl ethanol 96% at −20°C. To age birds that were not ringed as nestlings, we assumed that individuals captured for the first time were in their first year if they presented yearling plumage or in their second year if they presented adult plumage (e.g., Aparicio and Cordero 2001; Ortego et al. 2007a, b). We used pectoral thickness to estimate fledgling body condition (Aparicio and Cordero 2001), as it is more reliable than the residuals of body mass on tarsus length (Gosler and Harper 2000). Pectoral thickness was measured using a portable ultrasonic meter (Krautkrämer USM22F, Hürth, Germany; accuracy 0.1 mm).

Molecular analyses

We genotyped 394 Lesser Kestrels across 11 highly polymorphic microsatellite markers: Fp5, Fp13, Fp31, Fp46-1, Fp79-4, Fp86-2, Fp89 (Nesje et al. 2000), Fu1, Fu2 (J. Wetton, unpublished), Fn1-11, and Fn2-14 (Ortego et al. 2007d). All individuals were genotyped at all these 11 microsatellite markers. We used QIAamp DNA Blood Mini Kits (QIAGEN) to extract and purify genomic DNA from the blood samples. Approximately 5 ng of template DNA was amplified in 10-μL reaction volumes containing 1× reaction buffer (67 mM Tris–HCL, pH 8.3, 16 mM $(NH_4)_2SO_4$, 0.01% Tween-20, EcoStart Reaction Buffer, Ecogen), 2 mM $MgCl_2$, 0.2 mM of each dNTP, 0.15 μM of each dye-labelled primer (FAM, HEX or NED) and 0.1 U of *Taq* DNA EcoStart Polymerase (Ecogen). All reactions were carried out on a Mastercycler EpgradientS (Eppendorf) thermal cycler. The PCR programme used was 9 min denaturing at 95°C followed by 30 cycles of 30 s at 94°C, 45 s at the annealing temperature and 45 s at 72°C, ending with a 5-min final elongation stage at 72°C. Amplification products were electrophoresed using an ABI 310 Genetic Analyser (Applied Biosystems) and genotypes were scored using GeneScan 3.7 (Applied Biosystems). Tests for deviation from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium between markers were calculated following Weir (1996).

Parental genetic characteristics

The average genetic diversity of the zygotes was estimated using parental genotype information (e.g., Cordero et al. 2004; Hansson 2004). For this purpose, we used the similarity index described by Li et al. (1993) which has been proved to be an adequate marker-based estimator of relatedness in natural populations (Van de Casteele et al. 2001). This index is a good estimator of offspring genetic diversity and has been shown to be highly accurate compared to estimates where the observed offspring genotypes were used (J. Ortego, unpublished data). The rates of extra-pair paternity in the study population are very low (0.83%; J. Ortego, unpublished data) and so the potential errors derived from estimating offspring genetic diversity from parental genotype data are not expected to be an important problem in the studied system. Maternal and paternal genetic diversity was estimated using homozygosity by loci (HL), a microsatellite derived measure that improves heterozygosity estimates in open populations by weighting the contribution of each locus to the homozygosity value depending on their allelic variability (Aparicio et al. 2006). HL is calculated as follows: $HL = (\Sigma E_h)/(\Sigma E_h + \Sigma E_j)$, where E_h and E_j are the expected heterozygosities of the loci that an individual bears in homozygosis (h) and in heterozygosis (j), respectively. HL was estimated using CERNICALIN, an Excel spreadsheet available on request.

Statistical analyses

We first tested for directional changes in hatching success over the 16-year study period (i.e., from 1991 to 2006) using Generalized Linear Mixed Models (GLMMs) implemented with the GLIMIX macro of SAS (SAS Institute 2004). GLMMs allow analyses of data where the response variable is determined by both random and fixed effects. Hatching success (955 clutches) was fitted as dependent variable in a GLMM with binomial error and logit-link function. We included the number of hatched eggs as the response variable and clutch size as binomial denominator, allowing us to avoid information loss on the sample size from which the proportion of hatched eggs is estimated. In this analysis, we included year as continuous predictor, whereas locality was included as fixed factor. The identity of colony was included as a random effect to control for the possible non-independence of hatching success within colonies, in the manner of a randomized complete block design to avoid pseudo-replication (Krackow and Tkadlec 2001).

In the study period with available genotypic information and detailed data on parental phenotypic characteristics (i.e., from 2002 to 2006), we analyzed the factors affecting hatching success (236 clutches) using another GLMM with binomial error and logit-link function. We fitted as explanatory variables genetic terms (similarity index and maternal and paternal HL) and all non-genetic parameters (covariates: laying date, clutch size, mother's and father's pectoral thickness and age, colony size; fixed effects: locality, year) that could potentially influence hatching success (Serrano et al. 2005; Cordero et al. 2004). Once again, colony identity was included as random factor in this analysis. In spite of mate fidelity is low is Lesser Kestrels (J.M. Aparicio, unpublished data), some pairs constituted by the same members were monitored across years ($n = 5$). So, to avoid pseudo-replication we randomly included a single breeding attempt per pair in our analyses.

Initially, models were constructed with all explanatory terms fitted, including first-order interactions and quadratic effects to account for potential nonlinear relationships. Final models were selected following a backward procedure, by progressively eliminating non-significant variables ($P < 0.05$). The significance of the remaining variables was tested again until no additional variable reached significance. The result is the minimal most adequate model for explaining the variability in the response variable, where only the significant explanatory variables are retained. Hypotheses were tested using F statistics and all P values refer to two tailed tests.

Results

Annual average hatching success has increased by 14% over the 16-year study period, a mean 1% increase per year (Fig. 1). After controlling for the effects of colony identity (estimator ± SE = 0.020 ± 0.033; $Z = 0.60$; $P = 0.275$), hatching success increased significantly from 1991 to 2006 (estimator ± SE = 0.035 ± 0.012; $F_{(1,953)} = 8.63$; $P = 0.003$), but neither the effect of locality ($F_{(1,952)} = 0.30$; $P = 0.586$) nor the interaction between locality and year ($F_{(1,951)} = 0.96$; $P = 0.328$) were significant.

In the study period with available blood samples for DNA analyses and detailed data on parental phenotypic characteristics (i.e., from 2002 to 2006), average hatching success was 89%. During this period, we scored 394 Lesser Kestrels at the 11 microsatellite loci above described. The mean number of alleles per locus was 25.7 and ranged from 3 to 128. After applying sequential Bonferroni corrections to compensate for multiple statistical tests, four loci deviated from HWE (Fp13, Fp86-2, Fu2, Fn2-14). There was no evidence of genotypic linkage disequilibrium at any pair of loci (all $P > 0.05$). The proportion of hatched eggs declined and then increased significantly with colony size and was positively influenced by paternal age (Table 1). All other variables were not significant (Table 1). Quadratic terms and interactions between independent variables were all not significant ($P > 0.1$ in all cases).

Discussion

Here, we have documented a temporal increase of hatching success over 16 years in a wild Lesser Kestrel population experiencing a concurrent demographic and genetic recovery (Ortego et al. 2007c). Hatching failure declined from 22% in 1991 to 9% in 2006, which means a transition from an elevated hatching failure rate characterizing species that have passed a severe population bottleneck to levels generally reported for outbreeding bird populations (Koenig 1982; Westemeier et al. 1998; Briskie and

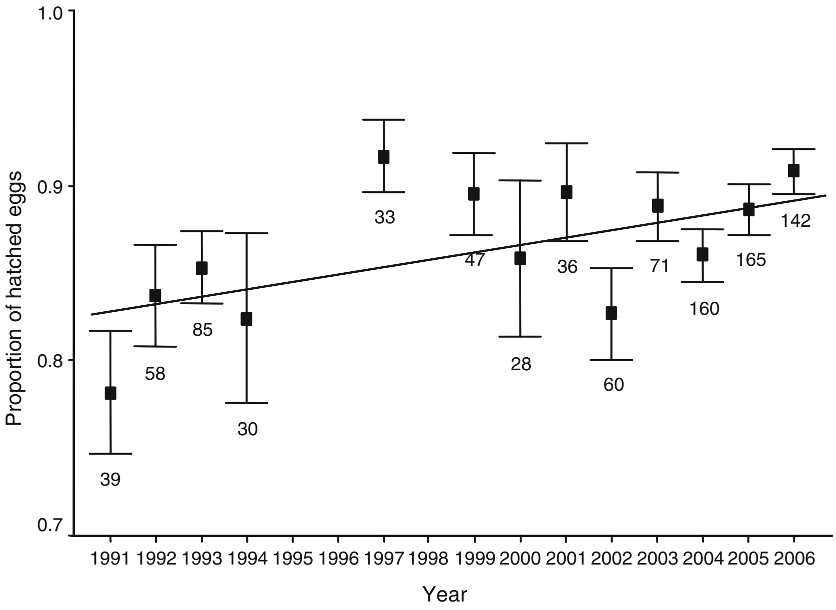

Fig. 1 Mean ± SE proportion of hatched eggs of Lesser Kestrel (*Falco naumanni*) from 1991 to 2006. *Figures under bars* indicate number of analyzed clutches each year. Proportion of hatched eggs increased significantly over this 16-year period (*regression line*)

Table 1 GLMMs (binomial error and logit link function) for hatching success of Lesser Kestrel (*Falco naumanni*) in relation to parental relatedness (similarity index), maternal and paternal homozygosity by loci (HL), and non-genetic terms

	Estimate ± SE	Test	P
Explanatory terms			
Intercept	1.719 ± 0.560		
Colony size	−0.105 ± 0.042	$F_{1,232} = 6.21$	0.013
Colony size^2	0.002 ± 0.001	$F_{1,232} = 7.11$	0.008
Paternal age	0.559 ± 0.181	$F_{1,232} = 9.57$	0.002
Colony identity	0	–	–
Rejected terms			
Parental relatedness		$F_{1,231} = 0.05$	0.826
Maternal HL		$F_{1,231} = 1.11$	0.293
Paternal HL		$F_{1,231} = 0.45$	0.501
Maternal pectoral thickness		$F_{1,231} = 0.28$	0.595
Paternal pectoral thickness		$F_{1,231} = 0.21$	0.646
Maternal age		$F_{1,231} = 0.23$	0.632
Clutch size		$F_{1,231} = 0.26$	0.609
Laying date		$F_{1,231} = 2.36$	0.126
Year		$F_{4,228} = 1.99$	0.097
Locality		$F_{1,231} = 0.09$	0.769

Colony identity was fitted as random effect

Mackintosh 2004). Additionally, in contrast to several studies that have found parental relatedness to be negatively associated with hatching success (Bensch et al. 1994; Kempenaers et al. 1996; Van de Casteele et al. 2003; Cordero et al. 2004; Hansson 2004; Barber et al. 2005), we found no relationship in the Lesser Kestrel study population during the years with available genotypic information.

Several factors could be responsible for the observed decline of hatching failure over years. The study population is not likely to have escaped from the generalized population crash registered for this species in the Iberian Peninsula in the 1960s to 1980s (González and Merino 1990). Such a population size reduction could have resulted in increased homozygosity that, in turn, may have initially increased the expression of the genetic load for hatching success (Briskie and Mackintosh 2004). Under continued inbreeding, deleterious recessive alleles could have been partially removed from the gene pool through the greater mortality rate of homozygous individuals, reducing the genetic load over years and increasing hatching success in successive generations (Barrett and Charlesworth 1991; Lacy and Ballou 1998; Crnokrak and Barrett 2002). On the other hand, the genetic recovery reported in the study area (Ortego et al. 2007c) could have diminished over time the risk that deleterious recessives alleles affecting embryological development come into a homozygote state and also may have led to increased heterozygosity at fitness loci submitted to balancing selection (Wright 1977; Charlesworth and Charlesworth 1987). Thus, although both immigration and mutations could have compensated selection against deleterious alleles, the temporal heterozygosity increase may have contributed to gradually reduce hatching failure over the study period (Lacy and Ballou 1998). Accordingly, several studies have reported enhanced fitness, including an increase of hatching success, in genetically depauperated populations after the introduction or natural arrival of immigrants that have contributed to increasing the genetic diversity of local populations (Westemeier et al. 1998; Madsen et al. 1999; Vila et al. 2003). Another possibility is that inbreeding depression experienced after the species population decline has selected for efficient mechanisms of inbreeding avoidance (Bensch et al. 1994). Also, as the population has grown, there may have been an increase in the probability that an individual finds a suitable mate with a genetic composition that complements its own genotype and maximizes their zygote heterozygosity at fitness-influencing loci (Bensch et al. 1994; Hansson et al. 2000). Finally, other non-genetic factors, such as better environmental conditions, increased food abundance, or lower pesticide use could also have contributed to reducing hatching failure over years (Negro et al. 1993; Rodriguez et al. 2006; Ortego et al. 2007e).

Similar trends between hatching success, genetic diversity and population size have also been reported for the endangered Greater Prairie Chicken (*Tympanuchus cupido*) over 34 years (Westemeier et al. 1998). In this species, hatching failure increased over years in line with a temporal decline in both population size and genetic variation. However, other studies have failed to find such a similar temporal pattern. Jamieson et al. (2003) reported increased levels of inbreeding in the threatened Takahe (*Porphyrio hochstetteri*) but hatching success did not experienced a parallel reduction over time. In this introduced population, founders were highly inbred and hatching success was consistently very low over years, suggesting that successive inbreeding could have not increased the expression of deleterious recessives probably due to a mutation-selection balance maintaining a constant genetic load for this trait over years.

Despite the observed temporal pattern of hatching rate, we found no effect of parental genetic characteristics on this reproductive parameter. Blood samples for DNA analyses were only available from 2002 onwards, the period in which values for hatching success became similar to those generally reported for non-inbred bird populations (Briskie and Mackintosh 2004). Partial purging of deleterious alleles and reduced expression of the genetic load over years due to the increased heterozygosity reported in the study population (Ortego et al. 2007c) could have attenuated the epistatic effects between loci that reinforce the negative effects of low genetic diversity. This may have reduced the power to detect genetic diversity–fitness correlations in recent years (Fu and Ritland 1996; e.g., Hansson 2004). Accordingly, Hansson (2004) found a decreasing effect of parental relatedness on hatching success over time in a Great Reed Warbler (*Acrocephalus arundinaceus*) population experiencing a demographic and genetic recovery similar to that reported in our study population (Hansson et al. 2000).

Our finding of no effect of parental genetic characteristics could also be the consequence of a low statistical power to detect genetic diversity–fitness correlations using a reduced number of neutral markers. The useful of neutral markers to estimate inbreeding coefficients or relatedness has been recently put into question on the basis of theoretical studies that suggest that a handful number of markers (5–15) is not likely to be informative of inbreeding and may lose important information on true relatedness (Balloux et al. 2004; Slate et al. 2004; Aparicio et al. 2007). Thus, even though we have analyzed an extensive dataset, the 11 neutral markers typed may have had low power to detect genetic diversity–fitness correlations. However, we have previously detected several correlations between different components of adult fitness and multilocus heterozygosity in our population, suggesting that inbreeding variance may be higher enough to detect genetic diversity–fitness correlations (Ortego et al. 2007a, b). Thus, regardless of several studies that have suggested that inbreeding depression is likely to be higher during early life stages (see "Introduction"), we were better able to detect heterozygosity–fitness correlations late in life. This may occur if alleles with purely detrimental alleles are only accumulated if their effects are confined to later life when selection against them is weak (Hughes et al. 2002). Thus, hatching success could show a lower genetic load than traits subjected to weaker selection, reducing the consequences of low genetic diversity and weakening even more the expected correlation between marker-based estimators of relatedness and early fitness.

The proportion of hatched eggs decreased and then increased with colony size. Higher colony size could increase behavioral interference due to social interactions and this may result in reduced hatching rate due to extended periods of parental absence during incubation (Koenig 1982). On the other hand, higher colony sizes may increase the chance of finding a genetically complementary mate at specific coding loci not analyzed here, which may reduce the negative effects of genetic incompatibility on embryo development (Ortego et al. 2008). Apart from colony size, male age also influenced hatching success, suggesting that male experience could be critical during incubation (Hamer and Furness 1991).

In conclusion, we found that hatching failure has decreased over time in a Lesser Kestrel population experiencing a concurrent demographic and genetic recovery. In contrast, parental genetic characteristic did not predict hatching rates in the last years of study when this trait reached values similar to those reported in non-inbred bird populations. Overall, these results indicate the importance of long-term data to evaluate population trends and suggest that relevant components of fitness can show rapid responses to increased genetic diversity and population size (Ortego et al. 2007c).

Zusammenfassung

Genetische Charakteristika der Eltern und Schlupferfolg in einer sich erholenden Population von Rötelfalken

Verminderte Schlupfraten sind bei Eier legenden Organismen häufig eine Konsequenz von Inzucht und wurden im Allgemeinen als ein nützliches Maß für die Auswirkungen einer reduzierten genetischen Vielfalt auf die Embryonalentwicklung betrachtet. In diesem Fall haben wir das Muster des Schlupfmisserfolgs in einer wilden Population des bedrohten Rötelfalken (*Falco naumanni*) untersucht. Im Detail analysierten wir in einem ersten Schritt die Veränderungen in der Rate des Schlupfmisserfolgs über einen Zeitraum von 16 Jahren (1991–2006) in der sich die untersuchte Population demografisch wie genetisch erholte und bestimmten daraufhin die Folgen der genetischen Charakteristika der Eltern auf den Schlupferfolg. Die Langzeitanalyse der Daten ergab einen signifikanten Rückgang der Schlupfmisserfolge über die Zeit. Der Schlupfmisserfolg ging von einer anfänglichen Rate, die für Arten typisch ist, die eine schwere Flaschenhals-Situation überstanden haben, auf ein Niveau zurück, wie es allgemein für nicht ingezüchtete Vogelpopulationen beschrieben ist. Für das beobachtete Muster könnten die teilweise Eliminierung schädlicher rezessiver Allele, der Anstieg der Heterozygotie im Lauf der Zeit, wie er in früheren Studien beschrieben wurde und/oder die Selektion in Richtung effizienter Inzucht-Vermeidungsstrategien verantwortlich sein. Im Gegensatz zu früheren Arbeiten fanden wir keinen Einfluss der genetischen Charakteristika der Eltern auf den Schlupferfolg. Obwohl wir einen großen Datensatz untersuchten, könnten die 11 typisierten neutralen Marker zu schwach gewesen sein, einen solchen Zusammenhang aufzudecken. Die genetische Analyse war außerdem auf die letzten fünf Jahre (2002–2006), in denen DNA-Proben für genetische Untersuchungen verfügbar waren, beschränkt. Während dieser Jahre lagen die Schlupfraten auf einem Niveau, wie es typischerweise für nicht ingezüchtete Populationen beschrieben ist. Ein fehlender Zusammenhang könnte mit einer Reduktion des

genetischen Materials erklärt werden, oder ist eine Konsequenz der genetischen Erholung, wie sie für die untersuchte Population für die letzten Jahre beschrieben ist.

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