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Effectiveness of vocal activities of the Lanner Falcon (*Falco biarmicus*) during breeding

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Abstract Detailed information is still lacking on structure and duration of calls of diurnal birds of prey as well on their vocal repertoire. The Lanner Falcon (*Falco biarmicus*) is considered a shy less-vociferous species but no quantitative data exist. Field evidence demonstrates that in the last decades this falcon did not improve its threatened status in Italy. We investigated call frequencies and their durations to ascertain the effectiveness of these signals, especially during the breeding season. In particular, if calls are honest signals about the genetic quality of males. We carried out this study during two breeding seasons in eastern Sicily where we monitored 25 nesting attempts at 19 breeding sites. During 114 observational sessions, we recorded (1) which sex uttered calls, (2) type of vocalisation (wailing and creaking calls) and (3) bird positions (flying or perched). In addition, we recorded duration of each vocal event because it seems to be significantly correlated with male quality. We checked nests annually to

ascertain the number, age and gender of nestlings. Lanner mates employ calls mainly in crucial reproductive stages (courtship, incubation, the first week after hatching and when young are fledging) optimising their efforts. In addition, males performing shorter vocal events produce broods significantly smaller in size and with a sex ratio biased towards females. In addition, they seem to desert the breeding site in the subsequent year. We suppose that in Italian fragmented breeding populations of Lanners, call structure and rates can predict population viability.

Keywords Vocal behaviour · Honest signalling · Call frequency · *Falco biarmicus* · Sicily

Zusammenfassung

Effektivität von Rufaktivitäten des Lannerfalken (*Falco biarmicus*) während der Brutsaison

Es gibt nach wie vor keine detaillierten Informationen über die Struktur und Dauer von Rufen tagaktiver Greifvögel sowie über ihr Lautrepertoire. Der Lannerfalke (*Falco biarmicus*) gilt als scheue, weniger lautstarke Art, doch quantitative Daten sind nicht vorhanden. Hinweise aus Feldstudien zeigen, dass sich der gefährdete Status dieses Falken in Italien in den letzten Jahrzehnten nicht verbessert hat. Wir haben Ruffrequenzen und -dauer ermittelt, um die Effektivität dieser Signale zu untersuchen, insbesondere während der Brutsaison. Wir haben uns besonders darauf konzentriert, ob die Rufe zuverlässige Signale sind, welche die genetische Qualität von Männchen anzeigen. Wir haben diese Studie während zweier Brutsaisons in Ostsizilien durchgeführt, wo wir 25 Brutversuche an 19 Brutplätzen beobachtet haben. In 114 Beobachtungssitzungen haben wir aufgezeichnet: (1) Geschlecht, das rief, (2) Ruftyp

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(„klagende“ und „knarrende“ Rufe) und (3) Position des Vogels (fliegend oder sitzend). Außerdem haben wir die Dauer jeder Lautäußerung aufgezeichnet, da diese anscheinend signifikant mit der Männchenqualität korreliert. Einmal jährlich kontrollierten wir die Nester, um Anzahl, Alter und Geschlecht der Nestlinge zu bestimmen. Beim Lannerfalken rufen Partner hauptsächlich in wichtigen Fortpflanzungsstadien (Balz, Bebrütungsphase, erste Woche nach dem Schlupf und Ausfliegen der Jungvögel) und optimieren ihre „Bemühungen“. Außerdem produzieren Männchen mit kürzeren Lautäußerungen signifikant kleinere Brutten mit einem zu Weibchen hin verschobenen Geschlechterverhältnis. Darüber hinaus verlassen sie anscheinend ihren Brutplatz im folgenden Jahr. Wir vermuten, dass in italienischen, fragmentierten Populationen des Lannerfalken Rufstruktur und Rufhäufigkeit Maße für die Qualität der Population sind.

Introduction

Generally, nesting territories of raptors are vigorously defended against intruders of the same or different species (see Newton 1979 and Simmons 2000 for reviews). In the early part of the breeding season, males perform conspicuous territorial displays (flights and calls) to attract females, informing at the same time other competitors about their motivational status (Jennions and Petrie 1997; Negro and Grande 2001). Noisy activities such as courtship aerial displays and copulations at the nest site should be efficient advertisements for neighbours about territory holders (Newton 1979). Thus, signals may encode different information about attributes of the sender such as paternal genetic quality but also about features of the location where territory holders are trying to reproduce (Maynard Smith and Harper 1995; Jennions and Petrie 1997; Penteriani et al. 2002; Forsman and Hagman 2006). In addition, these indirect signals strongly reduce dangerous aggressions towards intruders thus preventing potential injuries (Bonora and Chiavetta 1975; Negro and Grande 2001). In this way, increasing intensities and frequencies of specific signals displayed at different breeding stages should improve their effectiveness (Wiklund 1996).

Detailed information is still lacking on structure and duration of calls of diurnal birds of prey as well on their repertoire and effectiveness, especially during the breeding season (Sánchez 2007). Nonetheless, among large falcons, the Lanner (*Falco biarmicus*) is considered a shy less-vociferous species in comparison with the Peregrine (*F. peregrinus*), but no quantitative data exist (Wrege and Cade 1977; Leonardi 2001). Previously, Bonora and Chiavetta (1975) described almost ten call types uttered by Lanners during breeding. Although raptors often vocalise,

their repertoire of distinct calls is generally more limited than that of other birds (Negro and Grande 2001; Sánchez 2007). Distinctions between calls have often been based exclusively on the behavioural context rather than on spectral and temporal features (Bonora and Chiavetta 1975; Carlier 1995; White et al. 2002). In fact, few basic vocalisations have been identified in all intra- or interspecific interactions in sexual and territorial contexts of falcons (Wrege and Cade 1977; Hatzofe 1995; Sánchez 2007). Thus, previous studies on vocal communication in falcons used mainly vocalisation such as “wailing” and “creaking” calls for investigating male–female relationships or defensive behaviours during breeding (Rosenfield and Bielefield 1991; Carlier 1995). According to Sánchez (2007) vocalisations are loud and distinctive calls including one to multiple stereotyped elements related to different behavioural contexts. For instance, mating calls are also similar to alarm vocalisations and wailing calls are attended by antagonistic behaviour but also requests of food by the mate (Carlier 1995; Hatzofe 1995).

In Italy, several studies showed a continuous process of replacement of Lanners (ssp. *F. b. feldeggii*) by Peregrines, especially in sub-optimal breeding sites (Pellegrini et al. 1993; Manzi and Perna 1994; Magrini et al. 2001; Martelli and Rigacci 2003). Field evidence demonstrates that in the last decades Italian Peregrine populations notably increased while the number of Lanners apparently remained at least the same (Andreotti and Leonardi 2007; Andreotti et al. 2008). Thus, a sort of pressure upon Lanner populations exists and territorial behaviours including calls should be crucial for the defence of breeding sites against competitors (Holthuijzen and Oosterhuis 2004; Dekker and Corrigan 2006). Nevertheless, along the global range of the Lanner, the effectiveness of defensive and competitive behaviours towards other direct rivals (especially Peregrine subspecies) remains unclear when comparing Palearctic races and their successfully sub-Saharan counterparts (see Jenkins and Hockey 2001; Leonardi 2001 for reviews). Thus, investigations on performances of Lanner pairs is necessary and interesting for either sex, on the one hand for males, because of their higher variance in reproductive success (Griffith et al. 2002), and, in particular, if calls are honest signals about the genetic quality of males confirmed by productivity and persistence in subsequent seasons (Forsman and Hagman 2006). On the other hand, as suggested by the sex allocation theory, we can hypothesise that females bias the sex ratio towards male offspring according to the perceived attractiveness of their mate (Charnov 1982; Burley 1986; Anderson et al. 1997; Leitner et al. 2006).

This paper mainly aims at (1) determining how the frequencies of Lanner vocalisations vary at different breeding stages and (2) assessing the potential effectiveness of calls uttered by mates. In particular, we investigated if the

frequencies and durations of audible signals are related mainly to (1) the re-occupation of breeding sites and also to (2) the brood sex ratio and (3) paternal genetic quality.

Methods

Study area

We carried out this study during two breeding seasons (2003–2004), in a 4,769-km² area in eastern Sicily. From south to north, the study area is 73 km wide. The climate tends to be warm and dry especially in the southern parts, whereas rainy and sometimes snowy days are related to the north. As a consequence, the presence of different cultivation types follows climate conditions. Extensive wheat fields in the south are substituted northward by citrus groves and by olive yards. Natural vegetation interposes herbaceous steppe-like fields inside monoculture and Mediterranean shrubs in olive yards. Although the study area is far from the main cities, human presence comprises many small–medium villages and an extensive road network.

Preliminary observations

We searched for breeding sites before the beginning of the breeding season (September–November). Despite the large use of alternative breeding sites by Lanner subspecies (trees, buildings and electric poles), nests in Sicily are exclusively on rock faces (Leonardi 2001). We found and checked 48 nesting sites used at least once by large falcons including peregrines. All nest positions were recorded on a map (scale 1:10,000) using MapInfo 7.5 (MapInfo Corporation 2003). At the end of the study period, we recorded 25 nesting attempts by Lanner pairs in 19 breeding sites. In 2003, 33 % of breeding sites were deserted. This latter percentage increased to 61 % in 2004 with three rock faces (37 %) occupied by peregrines.

Data collection

We conducted 114 observational sessions of 5 h each with an average of 4.2 visits per site/season. During each session, 2–3 observers stayed on the base of the nesting site, with binoculars $\times 8$ –10. Observers were able to clearly distinguish behavioural patterns through a wide vision of surroundings. At least one experienced observer was involved in each session. Observations lasted from late January until the end of June, covering all breeding stages (courtship, incubation and young rearing) (Leonardi 2001). We set our observational sessions according to daylight duration: I (0600–1100 hours), II (1200–1600 hours), III (1700–2100 hours).

We categorised all vocalisations as (1) wailing calls and (2) creaking calls (Carlier 1995). The wailing call is a long and continuous call phonetically rendered as “*uèèh*” and the creaking call is a short sucking sound rendered as “*mciek*” for Lanners (Bonora and Chiavetta 1975), but they are not dissimilar from those uttered by other large falcons (Wrege and Cade 1977). As described in previous studies on Peregrines, calls often accompany advertisements made from prominent perching birds or were emitted during repeated rapid passes across the cliff face (Carlier 1995; White et al. 2002). Thus, during observational sessions, we recorded (1) which sex uttered calls, (2) the type of vocalisation (wailing and creaking calls), and (3) the bird’s positions (flying or perching). In addition, we recorded the duration of each vocal event because it seems to be significantly correlated with male quality (Catchpole and Slater 1995; Welch et al. 1998; Penteriani 2003). A vocal event consists of a series of syllables separated from the next one by at least 60 s of silence (Penteriani 2003).

We checked nests annually to ascertain the number and age of chicks and also to collect blood samples. We determined their age through a photographic guide (Kemp 1975), then we estimated the most probable week when the female laid eggs, which was also in accordance with our previous field observations database (1990–2000). In addition, we sexed nestlings using the intronic length variations between CHDW1 and CHD1Z genes (Brognia et al. 2005) to confirm if females should invest more heavily in male offspring according to the sex allocation theory (Charnov 1982; Burley 1986). We defined individual male quality through its productivity rates (brood size and number of fledged young; Catchpole and Slater 1995; Kroodsma and Miller 1996). Thus, we evaluated the effectiveness of vocalisations per nesting attempt/site/year in relation to two variables: (1) the maintenance of a nesting territory in the successive breeding season, and (2) the number of nestlings and young fledged. Our sample size was of 25 nesting attempts.

We recorded on tape 12 vocal events per three different breeding pairs ($n = 36$). For the sonogram analysis, we followed the audio treatment as in Sánchez (2007) using Raven 1.2 (Charif et al. 2004). Sound parameters including window type (hamming), window size (384 samples), frame length (512 points) and overlap (90.1 %). All measurements, including the lowest and the highest frequency (kHz), the difference among them (Δ frequency), the peak frequency (kHz) and the length in seconds of the signal (Δ time) were performed by Sonic Visualiser 1.7 (GNU General Public Licence, 2009).

Statistical analysis

We converted raw frequencies into relative frequency per h as number of calls/duration of observational session \times 60

(Carrier 1995). We used a non-parametric Mann–Whitney *U* test to compare relative frequencies of calls emitted during different breeding stages by both sexes, in relation to nesting site status (deserted or re-occupied by the Lanner in the subsequent year) and the number of young produced. All the tests were two-tailed. We avoid pseudo replications using the mean duration from each male for the analysis for non-parametric Mann–Whitney *U* tests and one way analysis of variance.

Results

Call structure

We analysed spectrograms of 36 vocalisations from three breeding pairs (Δ time 0.37 ± 0.23 s; males = 22, females = 14; Fig. 1). Frequencies ranged from 1.35 ± 0.40 kHz to 6.60 ± 1.27 kHz with Δ frequency 4.85 ± 1.27 kHz. Creaking calls are shorter (Δ time 0.28 ± 0.11 s) and higher pitched (1.40 ± 0.42 to 6.94 ± 0.94 kHz) than

wailing calls (Δ time 0.49 ± 0.29 s; frequency 1.28 ± 0.38 to 5.24 ± 0.87 kHz).

Call frequencies

We recorded 227 vocal events during 570 total hours of observation. We did not find significant differences in call frequencies, measured as relative percentage, among the daylight stages (I = 39.8 %; II = 31.5 %; III = 28.7 %; Chi-square test; $p = 0.08$). After courtship, females seems to be more vociferous than males by relative frequencies (Fig. 2). In fact, significant differences among sexes occurred during incubation (Mann–Whitney *U* test: $z = -2.323$, $p = 0.022$) and young rearing ($z = -2.757$, $p = 0.006$) periods but not at the courtship stage. In comparison with males, females uttered especially wailing calls (courtship, $z = -2.524$, $p = 0.012$; incubation, $z = -3.113$, $p = 0.002$; young rearing, $z = -4.210$, $p = 0.0001$) from perches or inside the nest (courtship, $z = -3.510$, $p = 0.0001$; incubation, $z = -3.992$, $p = 0.0001$; young rearing, $z = -4.176$, $p = 0.0001$).

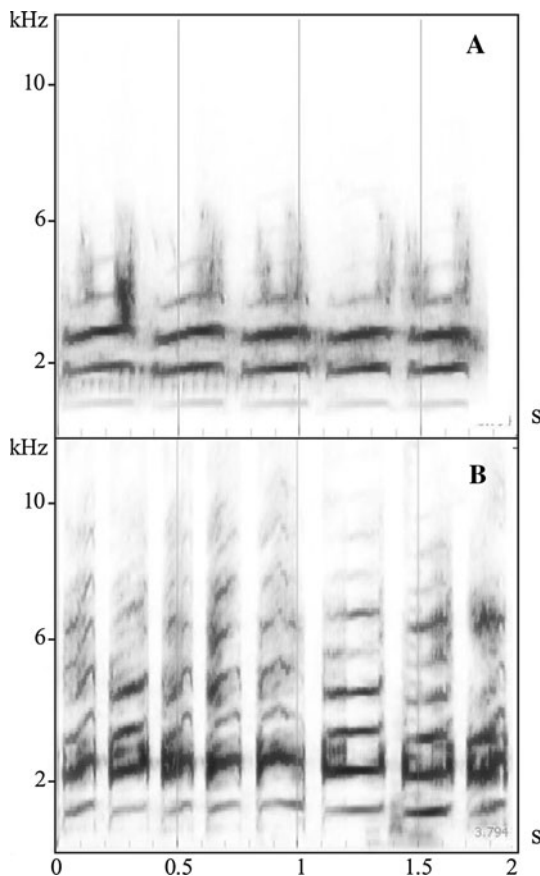


Fig. 1 Examples of wailing (a) and creaking (b) calls uttered by Lanners (*Falco biarmicus*) during the breeding season in eastern Sicily

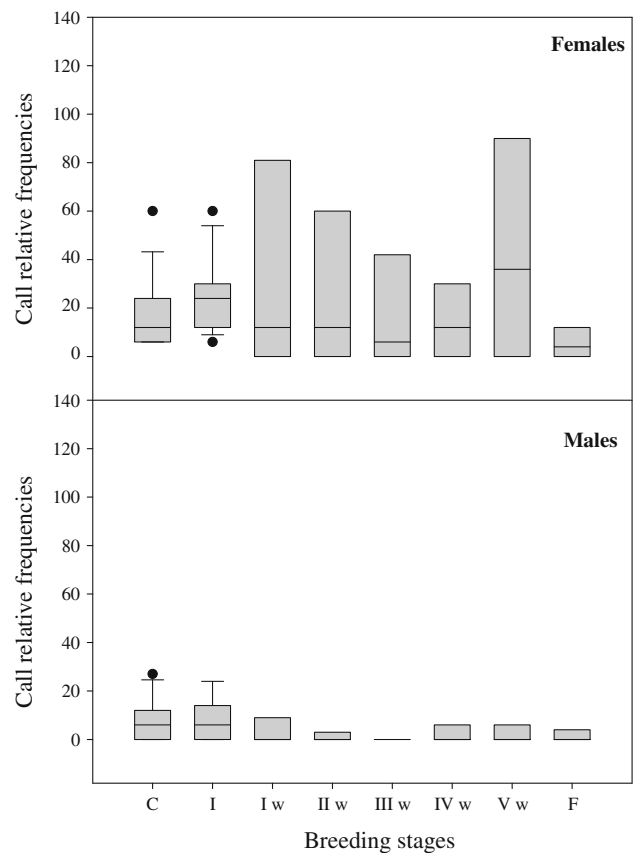


Fig. 2 Relative frequencies of calls made by males and females Lanner falcons during two breeding seasons in eastern Sicily ($n = 26$ nesting attempts; see text for details). C Courtship, I Incubation, I–V w ages of chicks by weeks, F fledglings

Table 1 Durations of male Lanner (*Falco biarmicus*) vocal events during the courtship period and means of nestlings and fledglings among re-occupied and deserted nesting sites in the following year

	$\bar{x} \pm \text{SD}$	Nestlings	Fledglings	Sex ratio (%)
Overall sample ($n = 25$)	38.2 ± 58.2	1.80	1.70	50.1
Re-occupied nesting sites ($n = 13$)	56.5 ± 85.7	2.40	2.10	63.0
Deserted nesting sites ($n = 12$)	25.3 ± 26.2	1.30	1.10	33.2

The sex ratio in percent indicates the mean proportion of the male sex in the brood

Conversely, creaking calls were not related to a particular sex. During courtship, males preferably vocalised in flight ($z = -2.692$, $p = 0.008$). We found no difference between uttering birds in flight during incubation. When young were ready to leave the nest at the end of the fifth week, mainly females emitted calls in flight toward them ($z = -2.298$, $p = 0.022$; Fig. 2). Finally, female call frequencies were positively associated with brood size during young rearing (ANOVA, $F_{2,25} = 6.184$, $p < 0.05$) and especially during incubation ($F_{2,25} = 17.206$, $p < 0.001$).

Effectiveness of calls

When we consider the overall dataset ($n = 25$), mean productivity is 1.32 fledged young per nesting attempts, with a balanced sex ratio (Table 1). Nevertheless, pairs which deserted breeding sites in the subsequent year have males performing shorter vocal events ($p < 0.01$), significantly fewer of fledglings ($p < 0.01$) and fewer male offspring ($p < 0.01$; Table 1).

Discussion

The Lanner belongs to hierofalcon complex, an assemblage of morphospecies not yet differentiated, which also includes Gyrfalcon (*Falco rusticolus*, Laggar (*F. jugger*) and Saker (*F. cherrug*) (Nittinger et al. 2005). In fact, the sound parameters we obtained from sonograms closely match those in the literature of Gyrfalcon (Wrege and Cade 1977; Booms et al. 2008). Inversely, genetic studies revealed a high genetic intraspecific diversity among Lanner races (Nittinger et al. 2005). In agreement, sonograms from North African *F. b. erlangeri* subspecies (Chappuis in Cramp and Simmons 1980) differ in peak frequencies (7–8 kHz) from our findings on the *feldeggii* race (6–7 kHz; Fig. 1). Probably, this dissimilarity also depends on habitat preferences by these subspecies, ranging from fragmented monoculture

fields (*feldeggii* ssp.) to more open environments such as sub- to hyper-arid lands (*erlangeri* ssp.). Nevertheless, our results are consistent with the Acoustic Adaptation hypothesis (AAH) and also recent data from other falcons (Morton 1975; Sánchez 2007). This hypothesis predicts that species living in more closed and cluttered habitats will have songs with lower frequencies and longer calls (Brown and Handford 1996). Conversely among other species inhabiting open habitats, Sicilian Lanner pairs produce short vocalisations ($\Delta\text{time } 0.37 \pm 0.23$ s; range 0.3 ± 0.3) with high peak frequencies (6.94 ± 0.94 kHz; range 9.2 ± 3.3 kHz) (Morton 1975; data range from Sánchez 2007). In this way, we suppose that the preference of males to vocalise in flight may also improve the perception of these signals from long distances.

This study represents the first quantitative analysis on vocal activities of the Lanner during breeding (Leonardi 2001). Our sample breeding population shows less temporal bias in daily pattern of vocalising as for wild Gyrfalcon, with a slight preference for early hours (period I: 39.8 % $n = 227$; Booms et al. 2008). As expected, this species seems to be less vociferous as relative frequency per h than the Peregrine, especially during courtship (Lanner = 0.4, Peregrine = 1.5; Carlier 1995). Nevertheless, pairs were not quite silent or shy as supposed by previous studies (Bonora and Chiavetta 1975; Leonardi et al. 1992). In addition, vocalisations should have an important role during different breeding stages as demonstrated by the allocation of activity frequencies (Fig. 2; White et al. 1994; Booms et al. 2008). For instance, females vocalise more than males except during the courtship period when they share efforts with their mates (Fig. 2). Thus, advertising of territory occupancy into the courtship stage becomes conspicuous during mating displays (Jennions and Petrie 1997; Negro and Grande 2001).

As in other studies, our breeding pairs with vociferous males have broods with more male offspring (Table 1; Burley 1986; Ellegren et al. 1996; Leitner et al. 2006). In wild populations of raptors with reversed sexual dimorphism (RSD), such as the Lanner, larger eggs produce males (Anderson et al. 1997). In fact, females may manipulate offspring sex and differentially allocate investment (i.e. yolk and testosterone amounts) to produce males from larger eggs with high growth rates and potential viability (Schwabl 1993; Gil et al. 2004; Leitner et al. 2006). Thus, females selecting mates with long calls should benefit indirectly through increased fitness of offspring (Table 1; Welch et al. 1998). In addition, females paired with more attractive males may also invest in more parental care (Burley 1988). In fact, females with larger brood size frequently vocalise (a costly activity) toward males during incubation and young development periods (Fig. 2).

The main aim of this paper is to assess if vocal activities of the Lanner improve the success of the reproduction and

the persistence of a breeding pair in a territory. Nevertheless, it is essential that this strategy is ultimately valuable in terms of costs and benefits. The energetic costs of calls are frequency-dependent, and therefore the vocalisations with the highest frequency are the most expensive for the birds (Roberts et al. 1983; Boncoraglio and Saino 2007). In fact, Lanner breeding pairs allocate calls mainly in crucial stages of the reproduction (courtship, incubation, the first week after hatching and when young are fledging) (Fig. 2). In particular, males become almost silent when they entirely provided food for brooding females. Conversely, females with eggs or chicks at early age frequently vocalise from the nest where they spend most of the daytime. Perhaps they are soliciting males to enhance their efforts in providing prey for the brood during this vulnerable period. These important differences in vocal frequencies among sexes are not reported for Peregrine (Carlier 1995), but are for other large falcons inhabiting open territories such as Prairie- and Gyrfalcons (Wrege and Cade 1977; Booms et al. 2008).

Our results suggest that long calls are honest signals in terms of the genetic quality of Lanner males (Table 1). In fact, the importance for males to advertise females about their status also occurred from call frequencies allocated mainly during courtship rather than in other periods (Fig. 2). Thus, males with longer vocalisations have better reproductive performances such as brood size and number of fledged young (Table 1). Nevertheless, some external factors, such as high densities, could mask the honesty of vocal event duration (Doutrelant et al. 2000; Penteriani 2003). Conversely, our breeding population is scattered in a wide area and pairs with poor males are more prone to disappear from breeding sites (Table 1). Laiolo and Tella (2008) suggest that depressed signalling affects the persistence of small local populations through low recruitment from other populations. As observed in a study on Lanners in Italy, each sub-population greatly depended on the size of nearby local populations (Andreotti et al. 2008). In fact, during our survey, we found nearly three sites per year occupied by adult unpaired individuals, mainly females. In addition, population size remains at least the same but pair distribution changed annually with many sites deserted or occupied by Peregrines (unpublished data from 2003–2008). Probably, as for other species with fragmented populations, call structure and rates better predict population viability of the Lanner (i.e. productivity; Table 1; Laiolo et al. 2008). Accordingly, females recognised male quality traits producing as expected more male offspring (Table 1; Burley 1986; Ellegren et al. 1996).

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