

HIGH PROPORTION OF NON BREEDING INDIVIDUALS IN AN ISOLATED RED-BILLED CHOUGH POPULATION ON AN OCEANIC ISLAND (LA PALMA, CANARY ISLANDS)

ELEVADA PROPORCIÓN DE NO REPRODUCTORES EN UNA POBLACIÓN INSULAR DE CHOVA PIQUIROJA (LA PALMA, ISLAS CANARIAS)

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SUMMARY.—*High proportion of non breeding individuals in an isolated red-billed chough population on an oceanic island (La Palma, Canary Islands).*

Isolated bird populations on oceanic islands may be good study models for the investigation of the interrelationships between social fractions of populations, especially due to their lack of long-range dispersal as a major mechanism influencing the dynamics and persistence of populations. We examined whether the ratio of breeders to non-breeders varies in a completely isolated red-billed chough (*Pyrhacorax pyrrhacorax*) population on an oceanic island (La Palma, Canary Islands) as compared to continental and other island populations, and assessed whether limited breeding opportunities may influence population crowding with non-breeding birds. The chough population in La Palma was composed of a proportion of non-breeders (about 60 %) representing twice the values reported in other populations. Most communal roosts were used during the breeding season by floaters sufficient in numbers to replace any loss among breeders. The average number of pairs nesting at several roosts did not differ between consecutive years despite much higher numbers of floaters using these sites throughout the year. The high proportion of non-breeding choughs suggests that nesting areas were saturated with non-breeding floaters due to some kind of limitation on breeding opportunities. Under conditions of isolation, limited breeding opportunities of floaters can not be eased by dispersing to other nuclei or vacant geographical areas outside the island, leading to a crowded non-breeding fraction. The dense chough population mostly composed of gregarious floaters in La Palma may be considered a guarantee of persistence and even future numerical increase. However, a low contribution of floaters to the effective population size compared with their contribution to the total population density may

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have repercussions in conservation by reducing the availability of essential resources for breeding pairs, which requires further research.

Keywords: Canary Islands, dispersal, floaters, isolation, La Palma, *Pyrrhocorax pyrrhocorax*.

RESUMEN.—*Elevada proporción de no reproductores en una población insular de chova piquirroja (La Palma, islas Canarias).*

Las poblaciones de aves aisladas en islas oceánicas pueden ser buenos modelos de estudio para investigar las interrelaciones entre las distintas fracciones sociales, debido a la ausencia de dispersión de larga distancia como mecanismo influyente en la dinámica y persistencia de las poblaciones. Examinamos la razón de reproductores/no reproductores en una población completamente aislada de chova piquirroja (*Pyrrhocorax pyrrhocorax*) en una isla oceánica (La Palma, islas Canarias) en comparación con poblaciones continentales y otras poblaciones insulares, valorando cómo las posibles limitaciones en las oportunidades de reproducción pueden influir en la superpoblación de aves no reproductoras. La población de chovas de La Palma está compuesta por una proporción de individuos no reproductores (60 %) que representa el doble de los valores registrados en otras poblaciones. La mayoría de los dormideros comunales fueron utilizados durante la época de cría por un número de individuos no reproductores suficiente para reemplazar cualquier pérdida entre los individuos reproductores. El número promedio de parejas reproductoras en varios dormideros comunales no difirió entre años consecutivos a pesar de la abundancia mucho mayor de individuos no reproductores que utilizaron esos lugares a lo largo del año. Los resultados sugieren que las áreas de nidificación estuvieron saturadas debido a algún tipo de limitación en las oportunidades de reproducción. En condiciones de aislamiento poblacional, la limitación en las oportunidades de reproducción no puede solventarse mediante la dispersión a otros núcleos poblacionales o áreas geográficas vacantes, dando lugar a una fracción no reproductora superpoblada. La densa población de chovas no reproductoras de La Palma puede considerarse una garantía de persistencia e incluso futuro crecimiento poblacional. Sin embargo, la reducida contribución de la población flotante a la población efectiva comparada con su contribución a la densidad poblacional total podría tener repercusiones negativas en su conservación mediante la reducción de los recursos esenciales para las parejas reproductoras, lo que requiere mayor investigación.

Palabras clave: aislamiento poblacional, dispersión, individuos flotantes, islas Canarias, La Palma, *Pyrrhocorax pyrrhocorax*.

INTRODUCTION

Populations of gregarious birds show complex social structures, often organized around interactions between breeders and non-breeders, including sub-adults and floaters, i.e. individuals that do not reproduce even though they may be physiologically capable of doing so (Brown, 1969). The proportion of floaters in populations varies with the availability of breeding opportunities that, in turn, depends on the availability of essential resources such as food, space, and mates (Newton, 1998). As a consequence of these potential limitations, floaters may delay reproduction in an attempt to en-

hance their future success (Zack and Stutchbury, 1992), which often means that they completely forego their own reproduction (Woolfenden and Fitzpatrick, 1984).

A surplus of floaters is expected to be associated with limited breeding opportunities (Zack and Stutchbury, 1992; Kokko and Sutherland, 1998), saturated breeding populations (Woolfenden and Fitzpatrick, 1984; Carrete *et al.*, 2006) and population persistence (Kenward *et al.*, 2000; Sarah *et al.*, 2004). Therefore, understanding the social structure of populations may have important conservation implications. For instance, the proportion of non-breeding floaters may influence popula-

tion dynamics by buffering mortality in the breeding population (Kenward *et al.*, 2000; Sarah *et al.*, 2004), but may also have negative consequences if non-breeders compete with breeders for limited resources (Kokko and Sutherland, 1998; Carrete *et al.*, 2006). Despite this potential importance of floaters in the stability and dynamics of populations, their role in the conservation status of endangered bird populations has received little attention (Kokko and Sutherland, 1998; Penteriani *et al.*, 2005; Sergio *et al.*, 2009), and little is known about the proportion of breeding and non-breeding individuals in different geographical areas or populations of particular species. This may be due to difficulties in estimating the size of the non-breeding fraction, especially in non-social species, because their dispersive movements may be unpredictable (Zach and Stuchbury, 1992; Koenig *et al.*, 1996; Rohner, 1996).

Isolated populations on oceanic islands may be good study models for the investigation of relationships between breeders and non-breeders due to the lack of long-distance dispersal as a major mechanism influencing the dynamics and persistence of populations. Dispersal in a metapopulation context may increase breeding opportunities for floaters if other population nuclei provide resources not available in the nuclei of origin (Serrano and Tella, 2003). On the contrary, floaters may increase in numbers in isolated populations, as often occurs on isolated oceanic islands (Nogales, 1994; Donázar *et al.*, 2002) due to the absence of long-distance dispersal. In these conditions of isolation, the proportion of floaters may depend on limitations to entry into the breeding population due to the availability of essential resources and the survival prospects of breeders and floaters, but not on opportunities to disperse to other populations or vacant geographical areas where essential resources for reproduction may be available.

In this study, we provide data on the size of the breeder and floater fractions in the red-

billed chough (*Pyrrhocorax pyrrhocorax*) population on La Palma, an oceanic island at the southwest limit of the global range of the red-billed chough (chough hereafter) and the only island inhabited by choughs in the Canary archipelago. Our primary objective was to determine the ratio of breeders to floaters on La Palma, and compare it with those of continental chough populations, where long-distance natal and breeding dispersal may connect different population nuclei or sub-populations characterized by different social and environmental features potentially influencing breeding recruitment of floaters (Banda, 2007). We also assessed relationships between the abundance of breeders and non-breeders in nesting areas also used as communal roosts by floaters during the breeding season to evaluate the potential limitation of breeding opportunities in a population completely isolated due to the lack of dispersal to other populations.

METHODS

Study species and study area

Choughs are medium-sized (*c.*300g), socially monogamous and sexually-dimorphic corvids that have declined in numbers, with local extinctions across their range in the Western Palearctic. They are social birds, joining flocks throughout the year that comprise mostly non-breeding individuals, which permits estimation of the size of the non-breeder fraction during the breeding season. Breeding pairs may nest isolated (usually in small cliffs, caves and artefacts) or in loose aggregations in large cliffs and gorges (Blanco *et al.*, 1997). Large cliffs used for breeding may be also used as temporal or permanent communal roosts, both by breeding and non-breeding choughs.

Chough distribution is highly fragmented in the western range with several isolated populations at the southern limit of their distribution, especially in Ethiopia and La Palma (Ca-

nary Islands). The distribution of choughs in the Canary Islands was greater in the past, as demonstrated by its presence in recent fossil deposits from La Gomera, Tenerife and probably El Hierro (Rando, 2007). Only occasional observations have been reported in recent times from La Gomera (58 km away from La Palma) and Tenerife (85 km away from La Palma and 28 km away from La Gomera) (Martín and Lorenzo, 2001). The chough population in La Palma has apparently decreased in numbers during recent centuries according to historic observations, and even during the last forty years (Martín and Lorenzo, 2001; Pais, 2005).

La Palma (28° 45' N, 17° 52' W; 708 km²) is the most westerly island of the Canary archipelago and the furthest from the African continent (416 km). Its volcanic origin and maximum altitude (2,426 m) result in a rugged topography with a variety of habitats (see details in Martín and Lorenzo, 2001). There are numerous caves and cliffs, and the abundance of suitable nest sites for choughs is apparently not limited, at least in the large cliffs and gorges used as communal roosting sites in both coastal and inland areas (authors' unpublished data). For instance, an evaluation of nest site availability conducted according to the methods described in Blanco *et al.* (1998) in two cliffs used by 12 and 14 nesting pairs showed five and seven times more potential than used nesting sites, respectively. In addition, choughs in La Palma nest in artefacts such as bridges, abandoned and used buildings, walls and even in trees, especially palms (*Phoenix canariensis*). These places, especially walls used in banana (*Musa cavendishii*) cultivars and trees, are an unlimited nest substrate in La Palma as there are multiple but unoccupied walls, palms and other trees located in suitable breeding habitat throughout the island (*pers. obs.*). Choughs in La Palma forage in all the island habitats, especially in cultivars and pinewoods (*Pinus canariensis*) at intermediate altitudes, scrublands (*Adenocarpus visco-*

sus) at the highest altitudes, and dry scrublands (*Euphorbia* spp., *Opuntia* spp.), grape vine (*Vitis vinifera*) and almond (*Amygdalus communis*) cultivars at low altitudes, but also in laurel forests and Monteverde (*Erica arborea*, *Myrica faya*) on eastern slopes. On La Palma, choughs included a predominant proportion of fruits and seeds in their diet throughout the year, especially those of the exotic *Opuntia* spp., Cactaceae (Pais and García, 2000; Pompilio, 2003).

Population monitoring

During October 2003 we located communal roosts by monitoring from vantage points and transects by car (totalling 1,450 km) the movements of choughs from foraging areas, located in all habitats around the island (Pais, 2005), to pre-roost gathering sites (places of aggregation regularly used just before entering the roost). In addition, we visited at least once during the afternoon all cliffs with potential to be used as communal roosts (i.e. gorges and isolated cliffs with vertical walls of > 15m height).

Once located, we conducted counts in all communal roosts in order to quantify the size of the winter population using standard census methods described in detail elsewhere (Blanco *et al.*, 2007). Briefly, the number of individuals at each roost was recorded from vantage points located at distances ranging from 30 to 100 m to the roost cliff, when birds arrived to the roost at sunset (Blanco *et al.*, 1993a, b). The counts of communal roosting individuals were conducted during periods of 6 - 9 consecutive days in October 2003, February 2004, October 2004 and January 2005. Censuses were performed simultaneously by three to six observers each day (a single observer at each roost) by covering, in a single afternoon, those geographical areas where communal roosts were located near each other (< 1 km from each other). Thus, we attempted to avoid any poten-

tial variation in the number of individuals at each roost between consecutive days due to possible changes in the use of roosts in close proximity (Blanco *et al.*, 1993a).

Although we recorded most (24 of 28) communal roosts in the first census (October 2003), the greater knowledge of the terrain and movements of roosting flocks acquired with time allowed us to establish with accuracy the total population size in the last and most complete survey (January 2005), when all roosts ($n = 28$) used sometime during the entire study period (2003 - 2005) were monitored (see Blanco *et al.*, 2007). During winter, all non-breeding individuals as well as a proportion of breeders joined diurnal flocks and communal roosts, with the greatest aggregations recorded in January in several Iberian populations (Blanco *et al.*, 1993a; Blanco and Tella, 1999; Blanco, 2003).

The size of the non-breeding population was determined by counting communally roosting individuals during the breeding season (May 2004 - 2005) at a sample ($n = 17$) of the same roosts used during the non-breeding season. During this period, the activity of breeding pairs provisioning nestlings and that of pairs that failed during incubation, which continue maintaining their nest-sites in the daytime during the breeding season, allowed us to distinguish them from non-breeding floaters joining flocks and arriving synchronously to the communal roosting sites at sunset (Blanco *et al.*, 1993a).

Breeding pairs at roosts were located with telescopes from distances ranging from 20 - 100 m, as both nests and roosts were on open cliffs. Each roost cliff also used as a breeding site was visited during daylight on several different days (3 - 16) during the breeding season (from laying in March-April to fledging in June) to locate all breeding pairs and to count the non-breeding individuals at sunset. The location of breeding pairs nesting outside communal roosts, generally in small cliffs, artefacts and trees (one pair per site and > 200 m to the

nearest pair) was recorded during the breeding season (2004 - 2005) but not censused exhaustively due to time and logistic constraints. We recorded whether pairs nesting outside communal roosts were confirmed breeding pairs or potentially breeding pairs ('pair present' and 'probable' categories) according to previously established criteria generally used in chough censuses (e.g. Bullock *et al.*, 1983; Blanco *et al.*, 1991; Finney and Jardine, 2003). Therefore, it should be considered as the minimum estimated breeding population outside communal roosts.

The proportion of the non-breeding population was calculated as the number of non-breeders at communal roosts during the breeding season (May 2004 - 2005) divided by the total population size during the non-breeding season (January 2005). In addition, a proportion of pairs nesting in places not used as communal roosts also use roosts during the non-breeding season (Blanco and Tella, 1999; Blanco 2003). This proportion may vary between populations and between years within populations depending on distance to the roosts, microclimate and protection against predators of nesting sites used as roost sites by pairs nesting there and, therefore, it could slightly influence the counts in communal roosts during winter (Blanco, 2003). To estimate this proportion we recorded the use of nesting sites at night during the winter of 2004 - 2005 of a sample of pairs ($n = 16$) breeding in areas not used as communal roosts (usually pairs nesting in isolation in artefacts, caves and small cliffs).

Limitation of breeding opportunities

To determine if breeding opportunities may be limited, we assessed the relationships between the abundance of breeders, breeding season floaters and all individuals at each communal roost during the winter. We assumed that breeding opportunities were limited when the number of potential breeders (floaters) exceed-

ed the number of breeding individuals in particular nesting areas (communal roosting sites also used as breeding colonies) to the point of allowing a potential turnover of the entire breeding fraction. These floaters should enter the breeding population by replacing losses in mated pairs or by establishing new pairs when new breeding opportunities arise (Kokko and Lundberg, 2001; Sergio *et al.*, 2009). We also compared the number of aggregated pairs nesting at several roosts in consecutive years to assess whether it remained constant in these particular nesting cliffs, providing additional, circumstantial evidence of limited breeding opportunities when a surplus of floaters exists in these sites (Woolfenden and Fitzpatrick, 1984). Non-parametric statistic was used due to the low sample size, nature and probability distribution of data.

RESULTS

Population size and proportion of floaters

We located 28 communal roosts used during at least one of the four census periods conducted during the non-breeding season (October 2003, February 2004, October 2004 and January 2005). Eighteen roosts (64.3 %) were used by choughs during all census periods, whereas the remaining sites were used temporarily across years and counts during the non-breeding season. Population size during the most complete census during the non-breeding season (January 2005) was estimated at 2,614 individuals (breeders and non-breeders) distributed across 21 roosts. The mean \pm SD size of the roosting groups during winter (January 2005) was 124 ± 20 (range = 44 - 370, $n = 21$).

We estimated that 124 - 139 breeding pairs nested on cliffs ($n = 18$) also used by floaters as roosts during the breeding season (three of these sites were used by breeders but not by floaters, see fig. 1a). At two other roosts located in inaccessible cliffs where estimating the number of breeding pairs was not possible, we

only counted the non-breeders arriving at the roost at sunset. Counts of all censused roost sites ($n = 20$) resulted in an estimate of 1,578 - 1,673 non-breeding individuals during the breeding season. Therefore, the minimum floating population represented 60.4 % - 64.0 % of the total winter population. This estimate of non-breeders was based on pooling counts conducted in May 2004 ($n = 9$) and/or May 2005 ($n = 16$), and the average counts in roosts sampled in both years ($n = 5$), because these repeated counts over two years revealed a similar number of individuals (Spearman rank correlation index, $r_s = 0.90$, $P = 0.04$, $n = 5$).

We recorded a minimum of 65 confirmed breeding pairs nesting outside communal roosts and estimated that 36 - 45 pairs more likely bred or were active at suitable nest sites during the breeding season. However, only a small fraction of the monitored breeding pairs nesting outside communal roosts used their nesting sites during the winter (12.5 %, $n = 16$ pairs).

Limitation of breeding opportunities

All roosts used throughout the year by floaters were also used as nesting sites by breeding pairs, whereas other roosts with fewer individuals were used by nesting pairs and floaters only during the non-breeding season (fig. 1a). The number of breeding pairs at each roost did not correlate either with the number of floaters during the breeding season (May 2004 - 2005, $r_s = 0.11$, $P = 0.65$, $n = 18$, fig. 1a) or the total number of individuals (breeders plus floaters) during the winter (January 2005, $r_s = 0.14$, $P = 0.57$, $n = 18$). However, most communal roosts were used during the breeding season by floaters in numbers sufficient to replace any loss among breeders nesting in these sites (fig. 1a). This was not caused by seasonal movements of floaters between areas, as suggested by the significant correlation between the number of floaters during the breeding season and the total number of individuals in the same

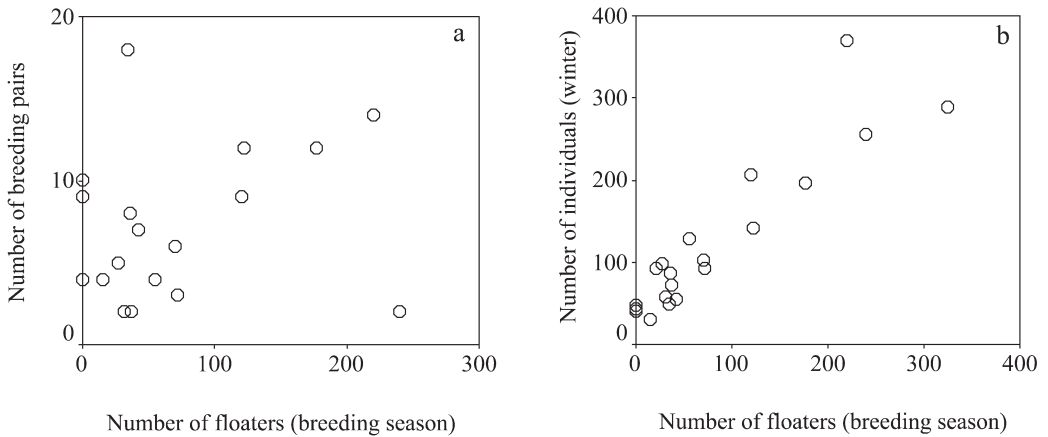


FIG. 1.—Relationships between the number of floaters attending each communal roost during the breeding season (May 2004 - 2005) and (a) the number of breeding pairs nesting on the cliffs used as communal roosting sites, and (b) the total number of individuals in winter (breeders plus floaters, January 2005) using the same communal roosts.

[Relaciones entre el número de individuos no reproductores en cada dormitorio durante la época de cría (mayo de 2004 - 2005) y (a) el número de parejas reproductoras en los mismos dormitorios, y (b) el número total de individuos en invierno (reproductores más no reproductores, enero de 2005).]

communal roosts during the winter ($r_s = 0.88$, $P < 0.0001$, $n = 20$, fig. 1b), and also because sampled roosts were located across the entire island. The number of pairs (ranging from 1 to 17) at several roosts also used by floaters (range = 37 - 240) did not differ between consecutive years (Wilcoxon matched-pairs test, $z = 8.5$, $P = 0.40$, $n = 7$).

DISCUSSION

Our results indicate that La Palma is one of the main strongholds of choughs in the Western Palearctic, with a population density of 4 individuals/km² considering the entire island. The high proportion of non-breeders (about 60 %) is the most striking social feature of this population. This proportion represents twice the values recorded in other populations (table 1), where the relatively fixed proportion of non-breeders around 30 % suggests that

floaters form a similar demographic fraction across populations, generally made up by juveniles and sub-adults 2 - 3 years old but also by older individuals (Still *et al.*, 1986; Blanco and Tella, 1999).

A high proportion of floaters may saturate breeding territories because floaters could rapidly replace any loss among breeders. In La Palma, most communal roosts were used during the breeding season by two to sixty times more floaters than breeders, a number apparently high enough to replace any loss among breeders nesting in these places. In addition, the average number of pairs nesting at roosts did not differ between consecutive years despite much higher numbers of floaters using these sites throughout the year. This suggests that nesting areas may be saturated with non-breeding floaters due to some kind of limitation on breeding opportunities. Whatever the underlying potentially limited resource, the absence of floater dispersal to other populations

TABLE 1

Comparison of the estimated proportion of the non-breeding fraction of the chough population in La Palma, Canary Islands with that from other studies in Europe. Population size indicates total number of individuals estimated in each region, on which the percentage of non-breeders was calculated.

[Comparación de las estimas de la fracción no reproductora de chovas en La Palma, Islas Canarias y otras regiones en Europa. El tamaño poblacional indica el número total de individuos estimados en cada región, sobre el cual la proporción de individuos no reproductores fue calculada.]

Region	Population size	% of non-breeders	Source
Scotland (mostly Islay)	184-340 ^a	26.0-35.4 ^a	Bignal <i>et al.</i> (1997), Cook <i>et al.</i> (2001), Finney and Jardine (2003)
Isle of Man (UK)	291-426 ^a	29.6-41.4 ^a	Bignal <i>et al.</i> (1997), Moore (2004), A. Moore com. pers.
Wales	390-451 ^a	27.0-27.2 ^a	Bullock <i>et al.</i> (1983), Bignal <i>et al.</i> (1997)
Ireland	1927-2627 ^a	31.2-31.5 ^a	Bullock <i>et al.</i> (1983), Berrow <i>et al.</i> (1993)
León (Northern Spain)	1681-1691	26.7-30.6	Baglione (1997)
Segovia (Central Spain)	1036-1084 (1376-1581) ^b	29.1-29.4	Blanco (2003)
SE Madrid (Central Spain)	898 (1000-1100) ^b	27.8	Blanco <i>et al.</i> (1991)
La Palma (Canary Islands)	2614 (2700-2800) ^b	60.4-64.0	This study

^a Variation between years.

^b Estimation of total population size (between brackets) due to the inclusion of breeding pairs not using communal roosts in winter, or estimated pairs without breeding confirmation and nest-site localization in areas not exhaustively censused (primarily inaccessible cliffs).

may further reduce the probability of floater recruitment as breeders, leading to an increased non-breeding fraction as compared with other island and continental populations interconnected by the movements of floaters (Roberts, 1985; Moore, 2006; Banda, 2007).

Dispersal may lead to increased mortality of floaters because of the risks associated with travelling and settlement in unknown areas where encounters with conspecifics may be unpredictable (Ruxton *et al.*, 1997; Dale, 2001). However, dispersal movements are not over long distances in La Palma because of the limitations imposed by island size. In addition, the encounters with conspecifics living at high population density and joining large and mobile flocks widely distributed around the entire island are very likely (Blanco *et al.*, 2007).

The establishment as breeders of choughs occasionally recorded in other Canary islands has apparently never occurred (Martín and Lorenzo, 2001), but their fate (death or return to La Palma) remains unknown. Thus, the large floating population may be partially a consequence of the apparent inability of floaters to 'escape' and establish themselves on other islands or continental areas, which may possibly likely increase survival but decrease breeding opportunities in comparison with other populations (Roberts, 1985; Moore, 2006; Banda, 2007). In this scenario, the contribution of a high proportion of floaters to the effective population size may be negligible, unlike their contribution to the total population density, which may guarantee population persistence or cause density-dependent reduction of breeding success

and population declines (Kokko and Sutherland, 1998; Carrete *et al.*, 2006).

Debate about priorities of conservation for isolated populations of rare species has focused on the number of breeding pairs as components of the effective population size or units for conservation (Meffe and Carroll, 1997). However, total or effective population size may be confounded by the social structure of populations, especially when breeding and floating fractions influence population trends differently (Kokko and Sutherland, 1998; Dale, 2001; Carrete *et al.*, 2006). Floaters may be considered an essential social resource for established breeders, and vice versa, when losses occur in mated pairs (Blanco and Tella, 1999). In fact, the flock has been highlighted as the central functional unit in population dynamics and conservation of choughs to the point that population declines may be associated with the loss or decline of flocks and the resulting disruption of the social organization (Bignal *et al.*, 1989; Bignal *et al.*, 1997). The dense chough population mostly composed of gregarious floaters in La Palma may be interpreted as a guarantee of persistence and even future numerical increase. However, this may require maintenance of a balance between the breeding and non-breeding fractions determined by unknown demographic parameters, especially because of the lack of dispersal. Given that choughs are social birds that tolerate, or cannot evict, floaters in their nesting and foraging grounds, the increase of floaters in relation to breeders may be limited by a density-dependent process regulated by the carrying capacity of the habitat (Kokko and Sutherland, 1998; Carrete *et al.*, 2006), of which a potentially differing magnitude for breeders (e.g. requiring essential nutrients for reproduction) and non-breeders (requiring nutrients for maintenance or failing to acquire enough essential nutrients for reproduction) remains to be explored.

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