Effective natal dispersal and age of maturity in the threatened Spanish Imperial Eagle Aquila adalberti: conservation implications

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Capsule Dispersive capacity appears sufficient to establish natural re-occupation of the former range.

Aims To document data on effective natal dispersal and age of maturity in the increasing, but fragmented, Spanish Imperial Eagle population.

Methods Between 1990 and 2002, 84 nestlings from six of the 14 breeding nuclei of the species’ range in Spain were tagged with metal and plastic leg-rings and radiotagged with VHF and satellite transmitters. Birds and breeding pairs were monitored annually throughout the distribution range for evidence of breeding status, movements, juvenile dispersal areas and behaviour prior to first-time pairing, establishment of a territory, and breeding.

Results The mean effective natal dispersal distance was 101.2 km and the median was 80 km (range 3–310, n = 12). Depending on how philopatry was defined, between 42 and 50% of individuals were considered philopatric. The majority of the philopatric individuals bred for the first time on the border of the breeding distribution range. Birds tend to breed first in the last area they inhabited. During their first breeding attempt, most eagles lay eggs and most have subadult plumage at this time. Birds were first recorded as being paired and territorial at a mean age of 3.4 years (n = 9), first egg-laying occurred at 4.5 years (n = 10) and first successful breeding at five years (n = 6). The earliest known breeding age was two years in females and three years in males.

Conclusion The dispersive capacity of Spanish Imperial Eagles appears sufficient to enable natural re-occupation of their former range. These results have important implications for the species conservation strategy, because the chance of contacting other breeding nuclei is greater than previously estimated and the natal dispersal distance has a relatively high colonizing capacity.

‘Natal dispersal’ is defined as the movement of an individual from its birth site to its first breeding site, and can be classified as either gross (the permanent movement of individuals to a new location regardless of whether or not they reproduce after dispersing) or effective (an individual reproduces following dispersal) (Greenwood 1980, Warkentin & James 1990, Belthoff & Ritchison 1990). Conversely, ‘breeding dispersal’ is defined as the movement of individuals between successive breeding places.

Two natal dispersal patterns in birds are considered: dispersive and philopatric (Greenwood 1980, Greenwood & Harvey 1982). Philopatry (i.e. individuals return to breed for the first time in the general area where they were born) is the most common pattern in birds. The causes of natal dispersal have been mostly related to two hypotheses: intraspecific competition for
resources (food, territory and mates), and the avoidance of inbreeding (Greenwood 1980, Johnson & Gaines 1990). However, there are notable variations in natal dispersal in different species, and even among populations of the same species subjected to different selective pressures (Weatherhead & Forbes 1994, Serrano et al. 2003, Cam et al. 2004).

In raptors, natal philopatry is the most common behaviour (Newton 1979). It has been found that a high percentage of Palearctic raptor species breed at sites less than 50 km from their birthplace (Galushin 1974, Forero et al. 2002); in philopatric species that usually breed in colonies, such as the Lesser Kestrel Falco naumanni, conspecific attraction strongly influences the probability of dispersal (Serrano & Tella 2003). Dispersive tendency has been described in species that live in temporarily fluctuating environments (Galushin 1974). Effective natal dispersal is among the most important demographic parameters influencing long-term trends and viability in raptor populations (Newton 1979), so it plays an important role in population dynamics and in the genetic structure of populations (Greenwood & Harvey 1982, Shields 1982, Johnson & Gaines 1990). For these reasons, knowledge of the type and characteristics of a species’ natal dispersal is important in order to estimate its capacity for population growth and geographical expansion.

Age of first breeding is an important component of lifetime reproduction in raptors, and the proportion of individuals that die without breeding increases each year that breeding is delayed (Newton 1989). Long-lived raptor species often exhibit prolonged periods of delayed maturity (Newton 1979); some of the individual variation in age of first breeding is related to favourable local conditions or to depleted populations leaving territories vacant (Newton 1977).

Spanish Imperial Eagles Aquila adalberti are large, long-lived raptors (birds 23 years old have been recorded; L.M. González et al. unpubl. data) that remain on their territories all year (González 1991). They are found only in suitable habitat areas that are difficult to access and situated far from human settlements in the southwestern part of the Iberian Peninsula (González et al. 1990). The range of Spanish Imperial Eagles decreased considerably during the 20th century (González et al. 1989b), dropping to a mere 50 pairs in the middle of the 20th century (Valverde 1960, Garzón 1972). The population has recovered to around 200 pairs and currently inhabits a range of around 117 000 km², distributed in patches of disconnected habitats which are considered to be breeding nuclei (González & Oria 2003). Nevertheless, it is considered an endangered species (BirdLife International 2004). There is limited published information on the age of maturity and natal dispersal (González et al. 1989a, Ferrer 2001). The only information available that could be used to understand effective natal dispersal in this species across the current geographic range comes from the results of a genetic study (Martínez-Cruz et al. 2004) in which the existence of low levels of population genetic structuring were detected, suggesting a probable exchange of individuals between breeding nuclei.

Ferrer (1993, 2001) assumed the entire Spanish Imperial Eagle population to be philopatric based on information from only one breeding nucleus (Doñana), which is small and peripheral to the main range, and it was proposed that the genetic exchange among breeding nuclei was so small that the population functioned as demographically independent subpopulations (Ferrer 2001, Madero & Ferrer 2002). This conclusion has been used to justify a project to create a new breeding nucleus outside of the breeding distribution range, via the re-introduction of young individuals (Madero & Ferrer 2002).

This paper describes for the first time the age of maturity and the characteristics of the effective natal dispersal in Spanish Imperial Eagles, and discusses the implications for some of the management and conservation measures currently in progress.

MATERIAL AND METHODS

Between 1990 and 2002, 84 nestlings from six of the 14 breeding nuclei of the species’ range in Spain, the most important breeding nuclei in terms of population size (González & Oria 2003) (see Fig. 1), were tagged with metal and coloured plastic leg-rings and radio-tagged with VHF and satellite transmitters, within the framework of the Actions and Recovery Plans of the species in the Autonomous Communities of Castilla y León, Madrid, Castilla-La Mancha and Extremadura.

The distribution range of the Spanish Imperial Eagle is shown in UTM 10 × 10 km quadrats in accordance with the ‘Spanish National Atlas of Breeding Birds’ (Martí & del Moral 2003). The breeding nuclei were formed by the union of the edges of the mesh made up of 10 × 10 km quadrats, with the presence of pairs displaying breeding behaviour (territorial defence, active nest) and their eight adjacent quadrats (see Fig. 1). The superposition of these groups of quadrats defined the edges of the nucleus mesh. It was considered that two occupied quadrats were located in the
same nucleus if they shared at least one of their adjacent unoccupied quadrats, and it was considered that two occupied quadrats were situated in different nuclei when there were at least two adjacent unoccupied quadrats between them. This criterion was based on the fact that the occupied quadrats contained up to five territories and their home-ranges could spill over into adjacent quadrats unoccupied by nest-sites (in particular where the nest was located near the edge of a quadrat). Also, the area of two empty quadrats was greater (on a pair level) than the average home range size of five radiotagged territorial individuals (5553 ha) (González et al. unpubl. data) and larger than the average distance between territories (González et al. 1990). Throughout the entire study the overall dimensions and number of nuclei remained similar, so we considered them valid for the period 1990–2002.

Thirty chicks were from the nucleus of Sierra de Guadarrama-Tietar River Valley, 13 from Sierra de San Pedro, five from Montes de Toledo and 32 from Sierra Morena (see Fig. 1). A total of 62 individuals (28 males, 34 females) were sexed by Wildlife Forensic Laboratory (Madrid) by the amplification of gene CHD-W according to the technique of Ellegren (1996). The tagged birds were monitored via satellite or conventional methods (light aircraft, vehicles). Intensive monitoring produced over 2400 resightings of these tagged birds, which provided basic information on the birds’ movements (González et al. unpubl. data). In this way we could detect the areas frequented by the radiotagged individuals. Moreover, in this context and using the same terminology of the nuclei (see Fig. 1 caption), we considered the penultimate area visited as the last area where the individuals were radio-located, before the first sighting in the area where they settled for first pairing, nest-building or egg-laying. Resightings of radiotagged individuals were made both in radio-monitoring locations whilst the transmitter was operative (maximum of five years) and in direct observations of PVC rings after the transmitter had run out. This, and the fact that most of the breeding population was monitored annually (González & Oria 2003), avoided bias towards birds that initially bred at younger ages as opposed to those that bred later but were not detected because their transmitter’s battery had run out.

Data on pairing and rearing were obtained via radio-monitoring, ringing data and nest monitoring. Most territorial birds and breeding pairs were monitored annually throughout the entire distribution range for data on the breeding status of tagged birds, movements, juvenile dispersal areas and behaviour prior to first-time pairing, establishment of a territory, and breeding (González & Oria 2003). In order to detect changes in the individuals of the pairs, we monitored annually the territories with observations conducted from prominent spots within the territory using 20–60× telescopes approximately 600 m from the nest. The eagles were identified individually on the basis of plumage differences, including the lesser wing-coverts, lesser scapulars and white shoulders (Hiraldo et al. 1976, González 1991, Forsman 1999), which differ between individuals and are present throughout life after successive moults without significant variations in extent or form (pers. obs.). In order to detect the formation of new pairs, on an annual basis we monitored the peripheral areas adjacent to the nuclei with potential habitat in accordance with the species’ nesting habitat selection criteria (González et al. 1992). In addition, we examined the recovery data of the 122 Spanish Imperial Eagles ringed in Spain, which are held at the Spanish Ringing and Migration Office (Madrid).

Evidence of maturity has been measured considering three types of behaviour categories. (1) Pairing with territorial activity. First-pairing was assumed when the paired eagle was seen with another eagle, either indicating an active breeding territory, or with a new partner presenting territorial behaviour, or when seen...
actively defending a territory against conspecifics and heterospecifics during the breeding period. We determined two types of pairing: substitution occurred when the tagged eagle paired with an eagle with a previously active territory (the vacancy was probably caused by the death or disappearance of the previous partner); and new pair was applied to a tagged bird that paired with another bird in an area where, during the regular annual censuses of the species (see González & Oria 2003), no eagles had been detected. (2) Nest-building. First nest-building behaviour was assumed when the eagles were observed bringing branches and other materials to the nest and the bird had been observed perched in the nest during the pre-laying period (December–February; González 1991). (3) Breeding (egg-laying). First breeding attempt was recorded when eggs or chicks were present in the nest. Successful breeding was recorded when young fledged successfully. Effective natal dispersal distance was the straight-line distance in kilometres between the natal nest of the tagged eagle (birthplace) and their first nest with eggs. In the case of first territorial settlement, we used the distance from the natal site to the usual roost or perches near to which territorial behaviour was observed. However, there were two cases (numbers 20 and 21, Table 1) in which, despite knowing the location where the birds were breeding regularly, it was impossible to establish precisely the year they first bred (eggs laid; F. Robles pers. comm.). Bearing in mind that in raptors pair formation is generally associated with nesting territories and potential breeding places containing nest-sites (Newton 1979), these two cases were not used when we calculated the age of maturity. However, they were used to determine the effective natal dispersal distance, because we assumed from our monitoring of the territory that the individual would not have changed its nesting place since its first breeding attempt.

The age of the individual was established in tagged eagles, considering 1 May of the year of hatching (the month when most hatching occurred; González 1991) as the individual’s first day of life. Bird age at maturity and effective natal dispersal were studied in all cases examined (via radiotagging recordings and recovery of rings).

The individual’s plumage and the associated age-class were determined as adult/definitive or subadult/transitional, according to the ageing–plumage identification guide classification established for the species (González 1991, Forsman 1999).

With the above information, we constructed Table 1 and, assuming that each case has the same likelihood of involving a change of pairing, location substitute or replacement, we considered all the cases as independent events (unless specified, they all included individuals with several cases or records; individuals numbers 3 and 11).

We used two approaches to measure philopatry. First, in accordance with Miller & Smallwood (1997), we used Shields’ (1982) definition of philopatry as the bird returning to an area within ten home-ranges from the natal site. In order to calculate this parameter, we used the average territory size of five radiotagged territorial individuals (5553 ha) (González et al. unpubl. data), which implies that the diameter of the territory is 4.22 km and the philopatric limit was therefore 42.2 km. Secondly, according to Serrano & Tella’s (2003) study of natal dispersal in birds, we used the term ‘philopatric bird’ when an individual bred within its natal nucleus (see above), and we considered the bird as dispersive when it bred outside the limits of its natal nucleus. Furthermore, in the cases of philopatric birds, if the breeding attempt occurred on the periphery it was considered to be peripheral philopatric. A peripheral philopatric case implied that the distribution range was increasing, whilst for other philopatric cases, the distribution range did not increase.

RESULTS

Effective natal dispersal

Mean and median effective natal dispersal distances (considering only the cases of egg-laying) were 101.2 ± 91.9 and 80 km (range 3–310, n = 12, Table 1) respectively. No significant linear correlation was found between the age at first laying and the effective natal dispersal distance (Spearman rank correlation, \( r_s = 0.006, \text{ns}, n = 10 \)). Effective mean natal dispersal distance in females (108.2 ± 84.35 km, range 22–255, n = 4) was similar to that in males (100.1 ± 79.56 km, range 3–310, n = 7, Mann–Whitney U-test, \( z = 0.19, P = 0.85 \)).

When we calculated the effective natal dispersal distances, including the cases of nest-building and territorial pairs, the mean and median distances were 84.4 ± 79.85 and 55 km, respectively (range 3–310, n = 18, Table 1).

Considering the cases of egg-laying, only five eagles (41.6%, n = 12) could be considered as philopatric according to Shields’ (1982) definition (Table 1), and considering all the broader criteria of maturity (paired,
Table 1. Evidence of maturity and natal dispersal in the Spanish Imperial Eagles radiotagged (case nos 1–16) and ringed (case nos 17–21).

<table>
<thead>
<tr>
<th>Case no.</th>
<th>Individual no.</th>
<th>Sex</th>
<th>Age</th>
<th>Evidence of maturity</th>
<th>Age class</th>
<th>Mate's age class</th>
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<td>M</td>
<td>3</td>
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<tr>
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Case No. | Natal dispersal distance (km) | Natal nucleus | Breeding nucleus | Pairing type | Location type | Nuclei visited | Penultimate nuclei visited |
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The breeding nuclei established in 2004 were: CD, including the Cotos de Doñana and Guadalquivir marshes; MOT, including the Sierras de Monfragüe and the Llanos de Trujillo; MT, including the Montes de Toledo; SA, including the Sierras de Almadén; SB, including the Sierras del Sur de Badajoz; SC, including the Sierras de Coria; SCO, including the Sierra Morena de Córdoba; SG, including the localities of Sierra de Guadarrama, Sierra de Gredos and Monte del Pardo; SGU, including the Sierra de Guadalupe; SMC, including the Sierra Morena central; SMR, including the Sierra Morena oriental; SP, including the Sierra de San Pedro; VG, including the Guadiana River Valley; VT, including the Tébar River Valley. See Fig. 1 for locations.

nest-building and egg-laying) only eight eagles (38.1%, n = 21) could be considered philopatric. According to Greenwood’s (1980) definition of maturity, nine eagles (50%, n = 18) displayed territorial behaviour (e.g. nest-building, paired and territorial defence) or bred in a different nucleus to that of their birthplace. Figure 1 shows how exchanges between different nuclei (determined by taking only the nuclei in which individuals...
were marked into account), occurred preferentially among the northernmost nuclei (SG, SP and MOT) and among the central nuclei (MT, SA and SMR).

The proportion of cases of new pairs and substitutions was equal (n = 10, Table 1) in the cases of egg-laying, but if all definitions of maturity are considered, the cases of new pairs are slightly higher (57.9%, n = 19). If only the cases of egg-laying are considered, most of the new pairs (81.8%, n = 11) settled on the periphery of the breeding nucleus, thus enlarging its area. All the substitution cases were produced inside the nuclei (n = 8).

Considering only cases of egg-laying, we found that new territory formation and substitution occurred in equal proportion (n = 19, Table 1). However, when the proportions in the northern (SG, SP, MOT, VT) and central (MT, SMR and SA) nuclei were analysed together, we found that in the northern nuclei, first pairings or breeding occurred more frequently via substitution (n = 6) than via new pair formation (n = 4), whilst in the central nuclei, new pair formation was more frequently recorded (n = 5) than substitution (n = 1), although the differences were not significant (Fisher exact test P = 0.59).

In cases in which areas were visited before the first breeding attempt (Table 1), on most occasions (77.8%) the individuals carried out their first breeding attempt in the location where they were last recorded before this breeding attempt. Most of the eagles (nine) visited the breeding nuclei regularly and only on three occasions did the individuals fail to leave their natal nucleus and breed in that same nucleus.

**Age of maturity**

We recorded the results of 19 instances of maturity in 21 Spanish Imperial Eagles (of which 16 were radio-tagged and five ringed), 12 males and six females. In ten instances they laid eggs, in six they occupied nests, and in three they paired and exhibited territorial behaviour (Table 1).

In most of the pairs, one or both individuals were subadults (94.1%, n = 17) and in 17 cases (89.4%) the marked individuals had subadult plumage. The percentage of males for which evidence of maturity was recorded in relation to the total number of radiotagged individuals of the same sex was significantly higher than that of females (75% versus 25%, χ²₁ = 4.78, P = 0.029), which means that fewer radiotagged females were recruited.

As shown in Table 1, the earliest known age of egg-laying for an individual was two years and the latest eight years, the mean age being 4.5 ± 1.75 years (n = 10, Fig. 2). The mean age of first successful breeding was 5.4 ± 2.06 years (n = 5). The earliest known age of breeding was two years in females and three years in males, and the latest was eight years in females and seven years in males. The mean age at first egg-laying was 5.2 ± 2.45 years for females (n = 3) and 4.17 ± 1.34 for males (n = 6). The mean age with first raised offspring was 5 ± 2.45 years (n = 3) in females and seven years in the only case observed in males. The first paired eagle was recorded at an age of 3.7 ± 0.47 years old (n = 3) and the first nest-building activity was recorded at a mean age of 3.7 ± 0.47 (n = 6).

Of the 19 cases in which we recorded the individual’s plumage class, 17 were subadults (eight egg-laying, six nest-building and three paired) and two were adults when first egg-laying. In the 17 cases in which we knew the mate’s plumage class, ten were subadult (five egg-laying, three nest-building and two paired). No differences were found between sexes with regard to the plumage classes of the mates (Fisher exact test, P = 0.338). On six occasions the mate’s plumage corresponded to an older age, even if it were subadult; on four occasions the birds had the same plumage, and on four occasions the mate’s plumage was that of a younger bird.

**Breeding dispersal**

In six cases we were able to follow the breeding attempts (until a maximum of three years after the first signs of breeding were observed). In four of these (individuals 4, 5, 6 and 7), the location of the place they first showed signs of breeding coincided with the subsequent ones, despite the fact that none of their first breeding attempts were successful, whilst in two cases (3 and 10), the birds changed location.

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**Figure 2. Age of maturity as determined by the proportion of eagles pairing up (●) and laying first eggs (□) as a function of age.**
DISCUSSION

Spanish Imperial Eagles are characterized by the delayed acquisition of adult plumage and the species begins breeding before the plumage is fully adult (Valverde 1960, González 1991). This occurs in several species of raptors, and delayed maturity has been interpreted as an evolutionary strategy to gain useful experience and increase individual fitness (Newton 1979). Adult plumage would then be interpreted as an indicator of an individual’s experience and ability to breed successfully. However, in most bird species, reproductive success appears to increase with age (Forslund & Pärt 1995) and in raptors it has been shown that mixed or young pairs have lower breeding success (González 1991, Penteriani et al. 2003). We found that in 50% of cases in Spanish Imperial Eagles, the first successful breeding attempt takes place in a new territory, probably because the highest quality areas are occupied and saturated by adults (González et al. unpubl. data). New subadult pairs are forced to settle in marginal and peripheral areas (González et al. 1990). This could explain why in Spanish Imperial Eagles, age and territory quality are interrelated and affect the birds’ reproductive success (Ferrer & Bisson 2003).

We have found that first territorial behaviour and nesting establishment, and the first evidence of breeding, occur mainly in individuals with non-adult plumage. Delayed acquisition of adult plumage is associated with deferred breeding (Newton 1979). An increase in resource availability (nest-sites or food supply) can boost the number of subadult breeders (Wyllie & Newton 1991, Broomer et al. 1998). On the other hand, an increase in adult mortality enables younger birds to breed (Balbontín et al. 2003, Ferrer et al. 2003). Based on the results obtained in the Doñana nucleus, it has been suggested that at least 10% of individual breeding eagles are subadult as a result of adult mortality, so it may be used as a reliable early warning signal of population decline (Ferrer et al. 2003). However, in most of the Spanish Imperial Eagles’ range it was common to find territories held by eagles in subadult plumage (27.6%, n = 112 in 2000; 33.3%, n = 132 in 2002; González et al. unpubl. data). The species’ current breeding population has been growing steadily since the 1980s, with an annual growth rate of 4% (González & Oria 2003). Thus, our data are not consistent with the suggestion for Doñana, but reflect the opposite pattern. Doñana is the only nucleus where the Spanish Imperial Eagle population is decreasing, and so this assumed early warning signal of population decline probably does not apply to the species in most of its range. For this reason, we suggest that the warning signal constituted by the increase of young birds as breeders (Ferrer et al. 2003) is applicable to the small and peripheral Doñana nucleus but not to the rest of the population, which is in an expansive phase (González et al. 1989b).

The estimated age at first breeding in long-lived raptors is three to four years old (Newton 1979, 1989); for example, in Bald Eagles Haliaeetus leucocephalus it has been estimated as three to four years old (Mulhern et al. 1994), in Golden Eagles Aquila chrysaetos as four years (Steenhof et al. 1983, Watson 1997) and in Lesser Spotted Eagles Aquila pomarina as four to five years (Meyburg et al. 2005). These results are similar to those obtained for Spanish Imperial Eagles (4.5 years), although the age range is very broad (two to eight years). Breeding by two years of age, as observed in some Spanish Imperial Eagles, has not been recorded for any other eagle species (Newton 1979). The earliest age at which raptors can breed appears to depend on the age at which they mature physiologically. According to Bell (1980), however, this probably occurs at an earlier age than that at which most long-lived birds breed for the first time. Food supply, mates and nesting places are constraining factors that may exert an important influence. Variations have been detected in the age of first breeding in raptor populations, depending on whether they are in decline or in an expansive phase (Evans et al. 1998, Bowman et al. 1995, Newton et al. 1989). Our results suggest that a low age of first breeding in Spanish Imperial Eagles also coincides with an expansive phase (González & Oria 2003).

Genetic studies of Spanish Imperial Eagles have differentiated two subpopulations, one in the Doñana area and the other in the rest of the current breeding range (Martínez-Cruz et al. 2004). However, our results consider the breeding nuclei as being based on the habitat occupied, and indicate that there was a more significant exchange of individuals between the northern nuclei (SG, SP, MOT) and between the central nuclei (MT, SA and SMR). This could suggest that both groups of breeding nuclei might function as subpopulations. This pattern of exchange is coincident with the direction in which the range of Spanish Imperial Eagles has expanded in the same period (González 1996, González & Oria 2003).

Our results, based on eagles from the species’ most important breeding nuclei, suggest that dispersive capacity appears sufficient to enable natural re-occupation of
its former distribution range, or at least the distribution that it had up to the middle of the 19th century (González et al. 1989b).

Our results also suggest that the chance of contacting other breeding nuclei is greater than previously estimated and that the natal dispersal distance has a relatively high colonizing capacity. This agrees with the conclusions of Martínez-Cruz et al. (2004), who proposed that there is no evidence of genome-wide genetic erosion in the Spanish Imperial Eagle, and dispersal between nuclei would appear to be sufficient to allow for genetic exchange, thereby reducing the deleterious effects of endogamy (Greenwood & Harvey 1982).

The actual expansion phase of the Spanish Imperial Eagles would appear to obviate the necessity of reintroducing eagles in areas outside their present breeding range. However, in the case of the Doñana subpopulation, we agree with suggestions in the Management Plan for Spanish Imperial Eagles in Doñana (PND 1992, Cadenas 1996), for recommended management measures to increase its effective population by reducing mortality and increasing productivity, and to minimize inbreeding by introducing individuals from other breeding nuclei (Martínez-Cruz et al. 2004).

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REFERENCES


