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Blind shots: non-natural mortality counteracts conservation efforts of a threatened waterbird

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Abstract

Waterbirds are particularly affected by the high hunting pressure they face in many regions, which in some cases is compromising conservation actions for threatened species. The marbled teal *Marmaronetta angustirostris* is one of the most endangered waterbirds in Europe. In order to restore its population, several conservation actions have recently been undertaken, including a population reinforcement programme in Spain using captive-bred birds. With the aim of assessing the success of the reinforcement programme to establish a long-term self-sustaining population, we identified mortality causes of marbled teal, evaluated the survival of individual birds of the reinforcement programme and estimated the viability of the population under different management scenarios. We used data from wild and captive-bred individuals tracked by GPS since 2018 ($n = 42$) and from a mark–recapture programme initiated in 2015 ($n = 297$). We recovered 15 dead birds or transmitters: 20% died of natural causes, 60% of non-natural causes (including all anthropic causes) and 20% of unknown causes. Furthermore, the GPS tags of 24 birds unexpectedly stopped transmitting without any indication of malfunction, and for 66.7% of these disappeared birds, the cessation was suspected to be caused by illegal shooting. Survival during the hunting season was higher for males (31.3%) than for females (12.5%), and for the wild (50%) than for the captive-bred birds (9.4%), probably due to differences in migration patterns to North Africa. Population viability models revealed that maintaining the breeding population at the current mortality rates is only possible with a permanent release programme of captive-bred individuals, and that in order to establish a self-sustaining population, non-natural mortality would have to be reduced by at least 40%. We recommend management measures to reduce marbled teal mortality, such as limiting legal hunting to hours with clear visibility, prosecuting illegal shootings, controlling exotic predators and improving water management to reduce disease outbreaks. Some improvements can be implemented in captive-breeding programmes, such as earlier release times and incorporating anti-predator training.

Introduction

Human impact has accelerated the loss of species worldwide in the last decades (Newbold *et al.*, 2015). Human population growth is increasing the pressure of human activities (e.g. energy generation, resource extraction, urbanisation, recreational activities) on wildlife populations (Venter *et al.*, 2016). In fact, reducing the impact of human activities is one of the greatest challenges for the conservation of threatened species (Brooks *et al.*, 2006). Hunting, both as a recreational and a food provisioning activity, is one of the human activities that can collide with biodiversity conservation (Brochet *et al.*, 2019). When well-managed, hunting can be compatible with biodiversity conservation (Perco, 2020). However, ineffective hunting regulations or their poor legal enforcement often lead to unsustainable or illegal killing of wildlife (Caro *et al.*, 2015; Amano *et al.*, 2017; Blanco *et al.*, 2019; Brochet *et al.*, 2019; Margalida & Mateo, 2019). This is seriously undermining the conservation of many species (Keane, Brooke, & McGowan, 2005), while also affecting ecosystem structure and functioning (Benítez-López *et al.*, 2017).

In Europe, hunting is mainly practiced as a legal recreational activity, however, illegal killing is widespread, with tens of millions of birds illegally killed every year (Brochet *et al.*, 2016, 2019; BirdLife International, 2017). Moreover, even when the hunting is legal, misidentification of the target species can affect non-target species when they are killed unintentionally. This is especially relevant when a threatened species can easily be misidentified as the target species or is forming mixed flocks with the target species (Blanco *et al.*, 2019), as can happen with waterbirds (Martínez-Abraín *et al.*, 2013). Waterbirds are among the wildlife most affected by legal hunting and illegal shooting in terms of impact on their global populations (Brochet *et al.*, 2016). Indeed, hunting pressure, together with wetland degradation, have led to the decline of many waterbird populations across Europe (Jiguet, Godet, & Devictor, 2012; Pöysä *et al.*, 2013; Lehikoinen *et al.*, 2016; Tjørnløv *et al.*, 2019; Fox *et al.*, 2020) where seven duck species are listed as threatened (Birdlife International, 2017). For these threatened species, both illegal shooting and the loss of individuals due to misidentification during hunting activities may jeopardise all conservation efforts. Moreover, concerning the conservation of threatened migratory waterbirds, it has been widely recognised that a flyway-level approach is critically important for establishing effective mitigation measures (Holopainen *et al.*, 2018).

Translocations and captive breeding programmes are some of the most widely used management actions to reverse the decline of threatened species (Seddon, Armstrong, & Maloney, 2007; IUCN, 2013), including waterbirds (Tavecchia *et al.*, 2009; Martínez-Abraín *et al.*, 2013; Reynolds *et al.*, 2012). The success of reintroduction and reinforcement programmes has been highly variable (Fischer & Lindenmayer, 2000; Fraser, 2008; Robert *et al.*, 2015). Furthermore, these programmes may also have negative effects on the native populations (Harrington *et al.*, 2013). Although these programmes are generally inadequately evaluated (Pérez *et al.*, 2012), their failure is mainly attributed to inability to mitigate the external pressures on wild populations (IUCN, 2013). A well-designed monitoring programme should accurately assess the behaviour of the reintroduced population in the wild and identify critical points that may compromise its viability (Pérez *et al.*, 2012; Berger-Tal, Blumstein, & Swaisgood, 2020). Precise identification of mortality factors and quantification of survival rates are essential to evaluate the effectiveness of conservation programmes (Tavecchia *et al.*, 2009; Badia-Boher *et al.*, 2019), allowing identification of appropriate measures for their improvement that could lead to successful conservation outcomes. In particular, waterfowl reintroduction programmes are subject to potential indirect effects of hunting and illegal shooting on their success.

In this study, we assess the population viability and causes of mortality of a severely threatened bird in Western Europe, the marbled teal *Marmaronetta angustirostris*. The European breeding population is estimated at a few hundred breeding pairs divided into two areas. The eastern population is restricted to one breeding site in Turkey and some records in Armenia and Azerbaijan, while the western population is mainly concentrated in only two wetlands in the southern Iberia where an estimated 50–100 pairs are present (Botella & Pérez-García, 2020). This species was the most abundant duck in many wetlands and marshes of the Iberian Peninsula and during the last half-century became critically endangered in Spain due to a decline in the breeding population and loss of breeding sites (Giménez, Botella, & Pérez-García, 2021). As part of the Spanish National Strategy for its conservation, a population reinforcement programme was started in 2001. Based on data from the reintroduction programme in the species' main breeding area in South-Eastern Spain, our objectives were to (1) evaluate the trend of the breeding population in relation to the reinforcement programme; (2) identify the main causes of mortality using data from GPS-tagged birds; (3) evaluate differences in mortality patterns between breeding and hunting seasons, (4) estimate the survival of captive-bred individuals using data from the long-term mark–recapture programme and (5) explore the population viability of the species under different reinforcement management scenarios using different numbers of captive-bred individuals and reduction of current mortality rates.

Materials and methods

Species and study area

The marbled teal is a medium-sized migratory duck that has a fragmented distribution expanding along the Mediterranean region to Western and Southern Asia. The populations of the western Mediterranean migrate for winter mainly to North-eastern Africa, while the populations in the eastern Mediterranean and South Asia migrate to the Middle East and Northwester India (Carboneras & Kirwan, 2020). A recent review of its population status in Europe showed a decline in reproductive pairs for the Mediterranean populations (Botella & Pérez-García, 2020). This decline has been related to destruction of breeding sites, loss of wetland quality involving frequent episodes of massive mortality (i.e. botulism) and illegal shooting (Carboneras & Kirwan, 2020; Giménez, Botella, & Pérez-García, 2021).

South-Eastern Spain (38.17°N, 0.75°W) contains the main breeding area for this species in Europe (Botella & Pérez-García, 2020). At present, marbled teals only breed at two marshes and a salt marsh, all of them being highly anthropised (Fig. 1). The main wetland in the area is El Hondo Natural Park, considered internationally a key site for the conservation of marbled teals, but also other endangered birds such as white-headed duck *Oxyura leucocephala*. The El Hondo Natural Park (23.8 km^2) is formed by two main irrigation water reservoirs and several small wetlands and ponds that are subject to various land uses, such as controlling water to supply irrigation for agriculture, outdoor recreation, hunting and fishing. The other two wetlands in the area are El Clot de Galvany Protected Area (3.6 km^2), a small marsh with recreational use where hunting is forbidden and

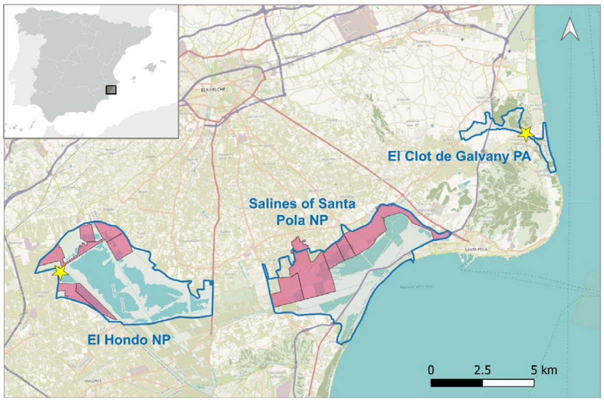

Figure 1 Map of the location of the wetland complex in South-Eastern Spain, also showing the locations of protected areas (blue line), hunting grounds (red areas) and the marbled teal release sites (yellow stars).

the salt flats of Santa Pola Natural Park (24.7 km^2) where waterfowl hunting and fishing is allowed in some of the surrounding small ponds (Fig. 1).

Spain has a long tradition of waterfowl hunting that is authorised even within some protected areas. The waterfowl hunting season in South-Eastern Spain usually starts on the second weekend of October and lasts until the second weekend of February of the following year. Some centuries-old practices are still used, such as the use of live decoys or massive provision of food to attract birds. According to current legislation, hunting is allowed even in low light conditions (i.e. between 90 min before sunrise and 90 min after sunset), which often hinders the correct identification of the game, potentially resulting in unintentional killing of protected species. In addition, the widespread poaching in the area exacerbates the problem (Pérez-García, Marco-Tresserras, & Orihuela-Torres, 2020).

Reinforcement programme

As part of the National Strategy for the conservation of the marbled teal, a population reinforcement programme was started in 2001 by the Regional Administrations. During the first years, it was an experimental project, but since 2013 it has been carried out consistently and systematically. This programme is defined as reinforcement because it implies the release of animals for reinforcing or re-establishing a local breeding population (Hodder & Bullock, 1997). Captive breeding is carried out at the Wildlife Recovery Center of El Saler (Valencia, Spain) from wild birds captured as chicks at the El Hondo Natural Park between 1994 and 1997. The birds are released employing a soft-release method, that is, 1-year-old birds are kept in a cage located on the shore of one of the protected lagoons for 3–5 days to become acquainted with the area, while food is provided. Once the birds have been released, the cage remains open until the next release group. The releases are usually carried out in groups of a maximum of 20 birds and between the end of February and April. All released specimens are marked with both metal and PVC rings with alphanumeric codes on their legs for remote reading.

In order to estimate the development of the breeding population, the regional government carries out specific intensive counts on all the wetlands of the region during the breeding season (May–July) since the start of the reinforcement programme in 2001. In addition, to obtain more detailed information on the survival of the released teals and to detect the presence of wild birds (un-ringed birds), an intensive periodic monitoring has been carried out at the three main wetlands in the study area from 2015 to the present. For this purpose, two types of methods were used. First, birds were actively searched using telescopes and binoculars. Second, to maximise readings of PVC-rings (Santangeli *et al.*, 2020), we installed a passive monitoring system by placing camera traps (Browning Strike Force Pro X 20 Mp) at the locations where teals usually rest out of the water. The cameras were checked periodically and the images were processed to look for ringed individuals.

GPS-tracking

Between 2018 and 2020, a total of 46 marbled teals (37 from the captive breeding programme and 9 wild birds) were tagged with GPS/GSM tracking devices. Marbled teals were captured for transmitter tagging using the release cage modified with a funnel so that birds could be trapped inside, except for 11 captive-bred birds that were tagged with the transmitters before their release. The cage-trap was baited with grain and visited daily during the trapping period. Trapping was carried out mainly at the end of the pre-breeding (May) and breeding seasons (July–September). Thirty birds were captured in the El Hondo Natural Park (6 wild and 24 reared in captivity) and five birds in El Clot de Galvany Protected Area (3 wild and 2 reared in captivity).

We used two different manufacturers of tracking devices, 13 tags from Ecotone (http://ecotone-telemetry.com/, Poland) and 33 tags from Ornitela (https://www.ornitela.com/, Lithuania). The transmitters weigh 9.5 and 10 g, respectively, which represent 2.0–2.6% of the weight of the birds, far from 3% which has been established as the upper limit to avoid effects on the survival or mobility of the individuals (Phillips, Xavier, & Croxall, 2003). Both devices are solar-powered and measure parameters such as external temperature, solar radiation and battery charge. Ornitela's devices also have an accelerometer that records the 3D movements. The transmitters were attached as a backpack employing a 4-mm-wide Teflon harness. The straps were crossed at the chest and stitched together to prevent movement of the device and finally tied to the back of the device, similar to Lameris *et al.* (2018). The transmitters were programmed to collect a GPS position once every 5–120 minutes, depending on the battery charge. GSM transmission was scheduled to occur once every 12 hr, except during the hunting season when a geo-fence was built around the hunting grounds so that marked birds entering the grounds would transmit once every 6 hr. Unfortunately, four of the transmitters malfunctioned in the first 2 days, and these birds were removed from the analyses.

Of the 42 birds whose transmitters worked successfully, 11 were aged as juveniles, 23 as on their second calendar year and eight as more than two calendar years old. Seventeen were sexed as females and 18 as males. The sex was determined using external features such as the colour of the bill and head shape and size (Green, 2000). For some juvenile birds, the sex could not be determined. The wild birds were aged according to plumage moult. See Table S1 in the Appendix for detailed descriptions of the tagged birds.

Identification of mortality causes

To study the causes and timing of mortality, we used data from the GPS-tagged birds as they provide a more precise data set than the capture–mark–recapture method (McIntyre, 2012; Klaassen *et al*., 2014). When the accelerometer data showed no movement for at least 12 hr, we assumed that the bird was dead, and we then immediately proceeded to search for and recover the body. Subsequently, the causes of mortality were determined through necropsy, classifying them into the following categories: natural causes (e.g. predation by native predators, disease, starvation), non-natural causes (including all anthropic causes and differentiating between illegal shooting and other causes such as collision with power lines or domestic cat *Felis silvestris catus* predation) and unknown (when decomposition or scavenging prevented the exact cause determination).

In some cases, the transmitter stopped sending information unexpectedly, which can be caused by a bird death in a poor coverage area, a transmitter failure due to external damage or a technical failure (Sergio *et al*., 2019). For each of the transmitters that stopped transmitting unexpectedly, we assessed whether these shutdowns were related to technical failures or malfunctions by reviewing changes in battery voltage, more intermittent or inaccurate fix transmissions or erratic temperature readings during the week prior to the signal disappearance (Murgatroyd *et al*., 2019). Except for the four transmitters that malfunctioned within the first tracking days, we did not observe any technical failure of the transmitters or a non-working tag on a live teal during the remainder of the monitoring period. We also did not recover any working transmitter detached from a teal. Therefore, we can assume that all transmission interruptions were related to the bird dying in an area with poor GSM coverage or the device being damaged at the time of death.

The GSM coverage is excellent in our study area, however, there was still the possibility of a dead bird being outside the coverage range (e.g. buried by a predator or a person). In addition, there is high probability that the transmitters are damaged on purpose, for example, when birds are killed by illegal shooting, it is likely that the perpetrators destroy the tags (Whitfield & Fielding, 2017; Murgatroyd *et al*., 2019). To determine in which cases unexpected transmitter shutdowns can be suspected to be related to illegal shootings, we compared the timing of the disappearances with hunting activities or with previous intensive use of hunting grounds by tracked birds (Murgatroyd *et al*., 2019). So, we considered as ‘suspected illegal shootings’ those birds that unexpectedly stopped transmitting inside a hunting ground or during a hunting day but the last tracked location of which was no further than 1 km from a hunting ground. Birds lacking evidence for a reason for stopping transmitting were assigned as ‘disappearance unknown’. This does not rule out that the bird may have died due to one of the above causes.

Survival estimates and population matrix models

To evaluate the differences in mortality patterns between different seasonal periods, we compared the survival of birds GPS-tracked during the breeding period (1st April to 31st August), with birds tracked during the hunting period (between 1st September to 31st March). The survival of GPS-tracked marbled teals was calculated using a modification of the Kaplan–Meier estimate (Pollock *et al*., 1989). We used Cox proportional hazards regression to model disappearance risk at the individual level to analyse the effects of the following factors: origin (wild or reared in captivity), sex (male or female), age (juvenile or adult) and year (to detect inter-annual differences) (Andersen & Gill, 1982; Heisey & Patterson, 2006). Models were compared using the likelihood-ratio test with ANOVA. All analyses were conducted with program R, version 3.5 (R Core Team, 2018). Cox regression was performed using the package ‘Survival’ (Therneau, 2015).

On the other hand, to obtain annual survival estimates from a larger number of individuals we used capture–mark–release–recapture models. We estimated the survival probabilities (φ) of 297 PVC-ringed marbled teals raised in captivity and released at 1-year-old between 2015 and 2019 while taking into account imperfect detection, that is, their resighting probabilities during the breeding season (ρ) between 2016 and 2020 (Lebreton *et al*., 1992). Goodness-of-fit (GOF) tests were used to assess the fit of the Cormark–Jolly–Seber model (φ_t ρ_t) to the data by using the program U-CARE (Choquet *et al*., 2009). The overall GOF test was not statistically significant indicating that the CJS model fitted the data adequately ($\chi^2_9 = 3.921,\ P = 0.917$). Thus, we tested for models considering constant and/or temporal variation in both survival and resighting using the program MARK (White & Burnham, 1999). Model selection was based on Akaike Information Criterion corrected by sample size AICc (Burnham & Anderson, 2002).

Stage-structured matrix projection models were developed to estimate the viability of the population under the current conditions and the potential effect of different management scenarios (Caswell, 2001). We used a two-stage (juvenile and adult) post-breeding census stochastic population model to represent the species life cycle and we simulated changes in demographic parameters and reinforcement numbers over time. The model included females only and assumed a 1:1 sex ratio at hatching (own data). Adult survival (S_a) was estimated using capture–recapture methods (see above) and juvenile survival (S_j) was obtained from the available literature (0.216 [0.002–0.41]; Green *et al.*, 2005). We assumed females reached maturity and began breeding at age 1. Fecundity (F) was estimated as $F = N_h \times S_0 \times F_r \times S_r$; N_h being the number of ducklings per female (see details in Appendix Figure S1), S_0 the duckling survival before independence (S_0; Oron & Gisis, 2006), F_r the proportion of females which reproduce and S_r the sex ratio considered as 1:1 (own data). Demographic stochasticity was included in the models using a random value of N_h according to the probability of laying a different number of ducklings per female, estimated from fieldwork (see Appendix Table S2); and the standard deviation of the survival estimates was used to randomly select values of S_a and S_j using a truncated normal distribution.

We used matrix projection to estimate the probability of quasi-extinction (defined as the number of females being ≤5). We simulated the population dynamics of five scenarios reflecting contrasting management strategies or the lack of them for 50 years. Scenario H0 represented the current demographic rates and no management actions. Scenario H1 represented the management of the population by releasing 1-year-old individuals with a balanced sex ratio of 1:1. H1.1 represented the release of 20 individuals per year during the first 10 years and H1.2 involved the release of 40 individuals per year during the first 10 years. We set this time limit (10 years) because reinforcements, like other conservation translocations, must proceed for a limited time. H2 accounted for a potential future reduction of mortality (average values), of 20% and 40% as H2.1 and H2.2 respectively. We assumed that these reductions would be applied to the fraction of non-natural mortality of the species. We ran 100 simulations for each scenario with an initial population size of 100 females (66 juveniles and 34 adults, based on the stable stage distribution of the stage-structured matrix model). Moreover, to assess the effects of adult survival on the extinction probability, the parameter S_a was varied over a wide range of values (0–1, with a 0.01 interval). We maintained the rest of the parameters and demographic stochasticity (Appendix Table S2, Figure S2), and we ran the model 100 times for each value.

Results

Quantifying reinforcement programme

From 2001 to 2020, a total of 612 marbled teals have been released into the wild in South-Eastern Spain. During the first 12 years, releases were irregular and sparse (range 0–21 birds per year and a total of 101 birds released), and concurrently, the number of breeding pairs in the wild has declined to their minimum in 2013 (Pearson correlation, $r = -0.65$; Fig. 2). From 2013 onwards, when captivity-breeding and releases have been carried out consistently and with a large number of birds per year (range 14–211), a slight increase in the breeding marbled teal population has been observed (Pearson correlation, $r = 0.92$).

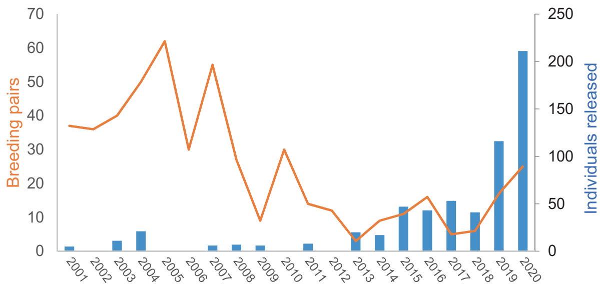

Figure 2 Numbers of breeding pairs of marbled teal in the Valencian Community (orange line) and numbers of marbled teals released by the reinforcement programme (blue columns) between 2001 and 2020. The data are provided by the regional government (Generalitat Valenciana).

Causes of mortality

Out of the 42 GPS-tagged marbled teals since 2018, only three birds remained alive at the end of the study period. We recovered 15 dead birds or their transmitters. Moreover, 24 additional transmitters stopped transmitting unexpectedly with no indication of any malfunction and the birds were never seen again (spatial locations of recovered dead birds or their transmitters and unexpectedly stopped transmitters are shown in Appendix Figure S3). Of the birds recovered, we determined the cause of death by necropsy or visual examination of their remains in nine cases (Table 1). Three marbled teals died due to natural causes, including one bird predated by a western marsh harrier *Circus aeroginosus* and one by an unknown carnivore, and another bird died of an undetermined disease. Six birds died of non-natural causes, two birds by shooting, two were predated by free-ranging cats, one died due to entanglement with the transmitter harness, and another one due to power line collision. Six other GPS-tagged birds or their transmitters were recovered. Although we were unable to perform necropsies on all of the birds or some of the results were inconclusive, we gathered some solid evidence regarding the cause of death in three cases. For these three birds, the accelerometer showed a sudden death, ruling out predation or disease. In addition, the event occurred inside a game reserve on a hunting day. Two transmitters were found with their harnesses intentionally cut off, while the third was recovered from an individual partially scavenged by rats, so the necropsy was inconclusive. Since in these three cases, we have evidence of illegal shooting, they were assigned to this cause of death. For the remaining three birds recovered, the cause of death could not be determined.

Of the 24 GPS-tagged birds that unexpectedly stopped transmitting, 16 had their last positions recorded within a hunting ground or during a hunting day, which has been considered as suspicious of illegal shooting (Table 1). For the eight remaining transmitters, we have been unable to determine the possible causes of transmitter failure, but they probably are related to true mortality, four of them being birds that disappeared in North Africa (3 in Algeria and 1 in Morocco; see appendix Figure S3).

Table 1 Summary of mortality causes of GPS-tracked marbled teals monitored in South-Eastern Spain between the years 2018 and 2021

		Natural mortality			Illegal shooting		Other anthropic causes				
Year	Tracked birds	Pred. raptor	Pred. carnivore	Disease	Conf.	Susp.	Power line collision	Pred. feral cat	Entangling harness	Unknown	Disappeared
2018	11 (0)				1	6					2
2019	14 (3)	1	1		4	4					4 (3)
2020	17 (5)			1		6 (2)		2	1	3 (1)	2 (1)
Total	42 (8)	1	1	1	5	16 (2)	1	2	1	3 (1)	8 (4)

We divided the causes of mortality into natural mortality, which includes predation (pred.) and diseases, and non-natural mortality, further divided into hunting and other causes. For illegally shot birds, we show the number of shot birds with confirmed necropsies or accelerometer analysis (Conf.) and the number of suspected cases where the birds disappeared inside a hunting ground or on a hunting day (Susp.). We also present the number of birds that died of other non-natural mortality causes or of unknown causes (Unknown), and the number of birds that stopped transmitting data for unknown reasons (Disappeared). The numbers for wild birds are shown in brackets.

Survival and modelling scenarios

Of the 22 birds GPS-tagged during the breeding season, only one bird died (Table 2). By contrast, of the 40 GPS-tagged birds alive at the start of any of the three monitored hunting seasons, only seven individuals (17.5%) survived until the end of the season. Interestingly, most of the survivors (5 of 7) moved out of the hunting study area during this season, to their non-breeding areas in North Africa (Table 2).

During the hunting season, GPS-tagged wild birds showed a significantly higher survival rate (50%) than captive-bred birds (9.4%; $\chi^2 = 4.32$, $P = 0.038$). Cox proportional hazards regression models found differences in GPS-tagged marbled teals' survival during the hunting season by origin ($\chi^2 = 5.4$, $P = 0.02$) and by sex ($\chi^2 = 4.0$, $P = 0.046$) but not by age ($\chi^2 = 0.9$, $P = 0.3$) or between years ($\chi^2 = 1.5$, $P = 0.47$) (Fig. 3). No differences in Cox proportional hazards regression models were found during the breeding season either depending on the origin, sex or age of the birds or between years (Fig. 3).

For captive-bred birds marked with PVC rings, capture-resight modelling also indicated that both survival and resighting probabilities were constant over time (Table 3). During the study period (4 years), annual survival of PVC-ringed teals was estimated at 0.466 (SE = 0.111, 95% CI = 0.267–0.676) and resighting at 0.133 (SE = 0.050, 95% CI = 0.062–0.264).

Viability analysis and management scenarios

We found that in the no management scenario (H0), that is, with the current demographic rates, the extinction of the population would occur in less than 50 years (Qe = 1; Fig. 4). Scenarios H1.1 and H1.2, in which management actions focused only on the release of captive-bred birds, showed a slight population growth when the action was being implemented (Fig. 4), but rapidly declined to extinction once the release of birds ceased (Qe values between 0.97 and 0.98 respectively). In contrast, in scenarios where non-natural mortality was curtailed, we found a decrease in Qe probabilities to 0.89 when the reduction is 20% (H2.1) and 0.13 when the reduction is 40% (H2.2; Fig. 4). The results of the variation in the probability of extinction as a function of adult survival indicated that there is a high sensitivity in the range S_a = 40–60%, where small variations in the adult survival rate lead to large variations in population viability. Moreover, adult survival rates of over 60% are able to reduce the Qe to almost 0 (see details in Appendix Figure S4).

Table 2 Summary of GPS-tracked marbled teals before and during the three consecutive hunting seasons (HS) in South-Eastern Spain

	Breeding season before HS		Hunting Season		
Hunting season	Birds at the beginning	Live birds at the end	Birds at the beginning	Live birds at the end and Location	Illegal shooting
2018–19	6	6	11	2 (1 SE Spain; 1 N. Africa)	7
2019–20	3 (3)	3 (3)	14 (3)	3 (3) (all in N. Africa)	8
2020–21	13 (4)	12 (4)	15 (5)	2 (1) (1 SE Spain; 1 N. Africa)	6 (2)
Total	22 (7)	21 (7)	40 (8)	7 (4)	21 (2)

We show the number of marbled teals tracked during the breeding season previous to the hunting season and at the beginning of the hunting season, as well as the number of tracked birds alive at the end of the hunting season (end of HS) and where the surviving birds were located. We also show the numbers of illegally shot birds (confirmed and suspected). The numbers for wild birds are shown in brackets.

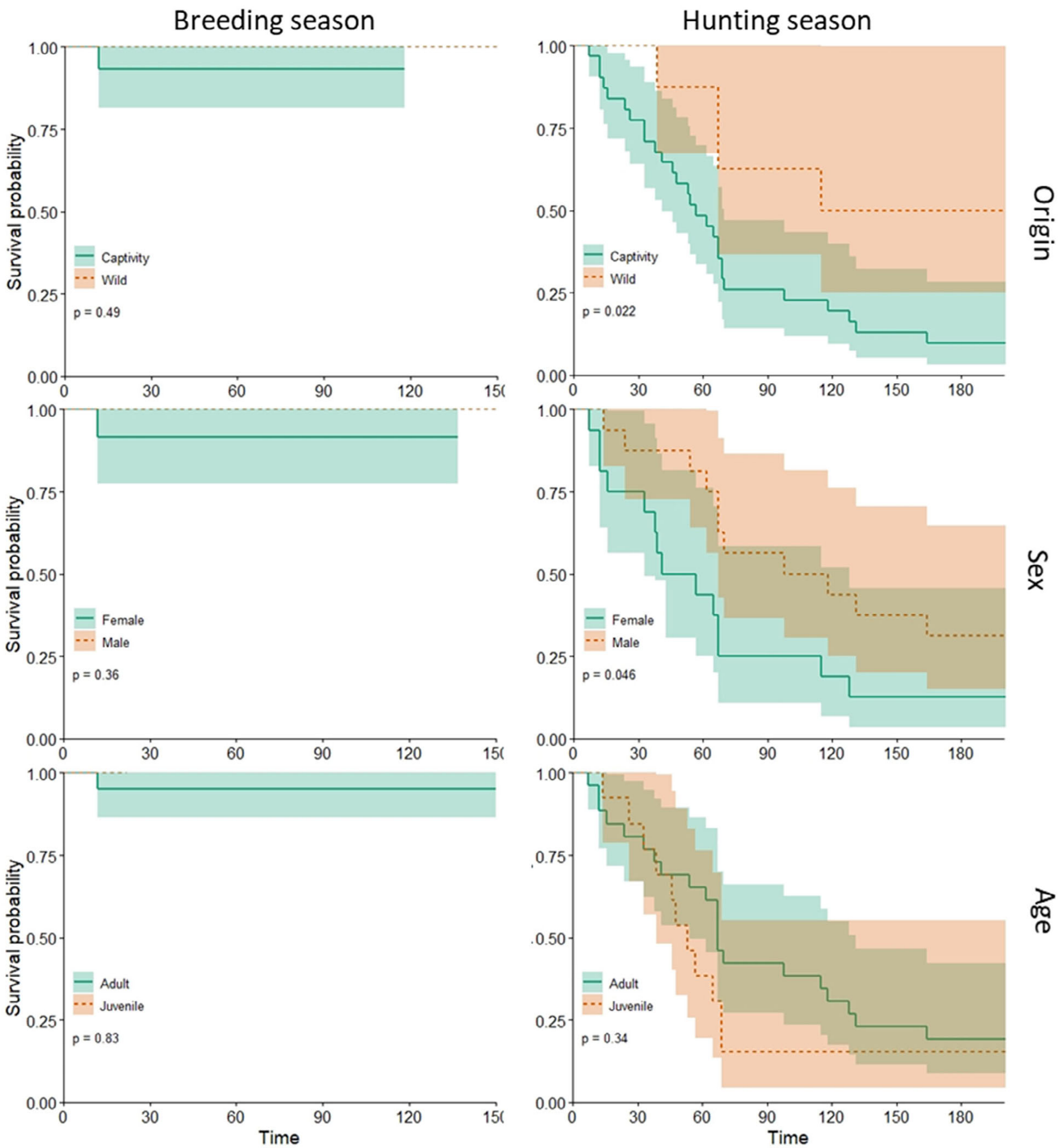

Figure 3 Survival probability of GPS-tracked marbled teals during the breeding season (1st April – 31st August; left-hand panels) and during hunting season (1st September – 31st March; right-hand panels). We analysed as factors the origin (wild or bred in captivity), sex (male vs female) and age (juvenile vs adults) of the birds. We show Kaplan–Meier log rank *P*-value from the score test.

Discussion

The combined use of GPS tracking devices, capture–recapture and population viability modelling allowed us to assess how the success of conservation actions can be undermined by the underlying impact of non-natural mortality. In the case of the marbled teal, our results support the fact that, primarily, the illegal killing of marbled teals is responsible for most non-natural mortality and is compromising the effectiveness of the reinforcement programme. Given the mortality rates estimated in this study, it is only possible to maintain stable breeding populations by a permanent release

Table 3 Model selection testing the effects of year (t) on local survival probabilities of marbled teals in South-Eastern Spain

Model	np	Dev	AICc	ΔAICc	*Wi*
$\varphi_{.}\ \rho_{.}$	2	20.694	214.594	0	0.952
$\varphi_{.}\ \rho_{t}$	6	19.759	221.896	7.301	0.025
$\varphi_{t}\ \rho_{.}$	6	20.280	222.417	7.822	0.019
$\varphi_{t}\ \rho_{t}$	9	16.893	225.349	10.754	0.004

np, number of estimable parameters; Dev, relative deviance; AICc, Akaike's information criterion adjusted for small sample size l; ΔAICc, difference between current model and the model with the lowest AICc; *Wi*, Akaike weight of model *i*; '.', no effect, that is, constant parameter.

programme of captive-bred individuals. Therefore, the ultimate objective of any reintroduction programme, which is the establishment of a self-sustaining population, would fail (IUCN, 2013).

Mortality causes and survival of marbled teals

In the case of the marbled teal, although there were previous indications of high mortality due to illegal shooting (Green, 1993, 2016), this is the first time that it has been possible to quantify its extent. Our data indicate that this is the most important cause of mortality, affecting a minimum of 33.3% of the population, although, based on evidence from birds that stopped transmitting on hunting grounds, this mortality could increase to at least 54% of GPS-tagged teals, affecting both teals released in the reintroduction programme and wild teals. We were not able to find similar studies using telemetry to compare our findings with other waterfowl in Europe, but in North America, mortality due to hunting (e.g. in mallards *Anas platyrhynchos*) ranges from 43% of mortality reported by Fleskes *et al*. (2010) to 85% described by Yetter *et al*. (2018) or 91% from Fleskes *et al*. (2007). Similar values have also been observed by studies using analyses of ring recoveries of mallards in northern Europe (Gunnarsson *et al*., 2008; Söderquist *et al*., 2021).

In South-Eastern Spain, other anthropogenic causes also seem to generate loss of individuals, for example, collisions with infrastructures (i.e. power lines) or predation by cats. In particular, predation by free-ranging cats seems to be an emerging threat that should be carefully considered (e.g. Medina & Nogales, 2009; Piontek *et al*., 2021). Although in our study area, we recorded only two confirmed events (13.3%), in another area of reinforcement releases of captive-bred birds located in central Spain, we recorded a minimum of four marbled teals predated by cats out of eight GPS-tagged birds (50%; own data). The presence of free-ranging cats in wetlands seems to be bolstered by the increasing anthropisation of these habitats, through the establishment of new housing settlements, growing tourism and recreational use and the presence of feral cat colonies on the edge or even within protected areas (Vanek *et al*., 2021; Orihuela-Torres, Sebastián-González, & Pérez-García, 2023).

Although only one mortality case due to disease was found during our study, botulism and other epizootic outbreaks have periodically been recorded in the El Hondo Natural Park causing mass mortalities (Green, 2016). The marbled teal appears to be sensitive to botulism because it is a late-breeding species, with its breeding season coinciding with the time when these outbreaks are most frequent (Fuentes *et al*., 2004; Anza *et al*., 2016). Although these outbreaks are natural, they are generally mediated by human activity, for example, due to changes in water levels and increasing eutrophication (Vidal *et al*., 2013; Anza *et al*., 2014).

The use of GPS tags has made it possible to accurately identify sources of mortality, even in difficult instances such as illegal shootings. However, these devices could potentially cause some adverse effects on waterbirds, including reduced survival probabilities and increased susceptibility to particular

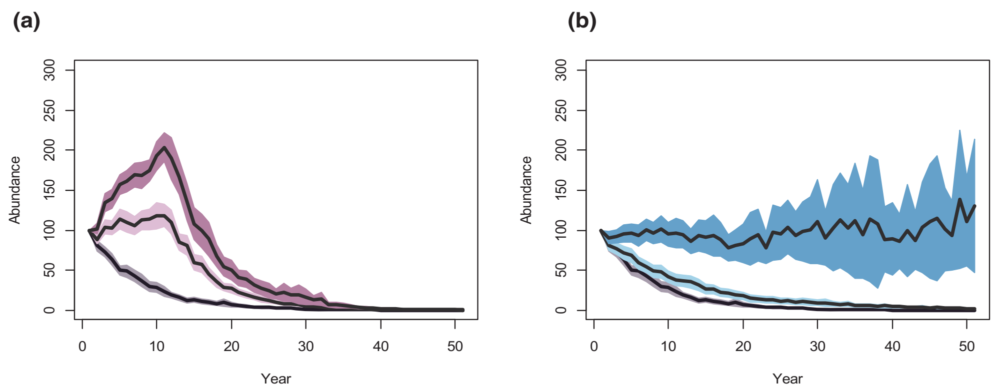

Figure 4 Population dynamics of marbled teal under current demographic rates and without (H0, in grey) and with different management actions. (a) Scenarios of release of individuals: scenario H1.1 (release of 20 individuals during the first 10 years of the period) in light purple and H1.2 (release of 40 birds during 10 years) in dark purple. (b) Scenarios of reduction of mortality: scenario H2.1 (reduction of 20% of mortality) in light blue and H2.2 (reduction of 40% of mortality) in dark blue. The simulation time span was 50 years and 100 replicates were carried out. The black line for each scenario represents the average number of individuals across all the simulations, and the shaded areas show the 5% and 95% confidence intervals.

causes of mortality (see review in Lameris & Kleyheeg, 2017). In fact, although the 95% CI of survival probabilities of captive-bred birds marked with PVC rings estimated by capture–recapture models overlap with those of the GPS-tagged individuals estimated by Cox proportional hazards regression models, mortality probabilities seem higher for GPS-tagged birds (see results). Accordingly, and in order to be cautious, we used the '"more optimistic' survival rates estimated by capture–recapture models to infer population dynamics under different conservation scenarios.

Our results on GPS-tagged marbled teals did not show lower survival for females than males during the breeding period, as has been found in many other waterbird species (Johnson, Nichols, & Schwartz, 1992). This could be related to the low predation pressure in the study area during the breeding season (Orihuela-Torres *et al*., 2022). However, we detected sex-dependent differences in survival during the hunting season (31.3% in males vs. 12.5% in females). These differences could be related to the effect of GPS-devices on the birds. Males being larger than females can better support the additional weight of the transmitters. However, the differences could also be related to the difference in reproductive energy expenditure between the sexes.

The life history strategy of marbled teals includes high reproductive rates, reproduction already in their first year of life, short lifespan and dispersal movements, probably linked to avoidance of high predation pressure or low resource availability (Green, 2016). Hence, in some cases, human-related mortality such as illegal shooting could be compensatory, if the illegally killed birds belong to the fraction of individuals that would have died naturally (Sandercock *et al*., 2011), which could be the case, especially with captive-bred birds because their survival probability in the first year of life has been artificially increased by having been bred in captivity. In fact, due to captive breeding, they may also be more vulnerable to predation or starvation (Berger-Tal, Blumstein, & Swaisgood, 2020). Moreover, differences in migratory behaviour between wild and captive-bred birds may explain their differences in survival, as has been identified in other duck species (Champagnon *et al*., 2012; Söderquist, Gunnarsson, & Elmberg, 2013; Söderquist *et al*., 2021).

Survival pressures are not homogeneous throughout the year for ducks, and they tend to suffer higher mortality rates during the post-reproductive and wintering periods (Baldassarre & Bolen, 2006). This is consistent with our data, as we observed a higher seasonal survival rate for GPS-tagged marbled teals released during the breeding season than in the non-breeding season (0.95 vs. 0.18). This increase in mortality rate during autumn and winter can be explained by several factors: increased predation pressure (mainly by wintering raptors (Pérez-García, Marco-Tresserras, & Orihuela-Torres, 2020)), reduced availability of food resources, the onset of risky dispersive and nomadic movements, and, of course, hunting pressure. In addition, potential harmful effects of GPS-tags could be making tagged individuals more susceptible to the different types of mortality mentioned above, for example, predation. This may partially explain why the survival rate recorded in our study during the hunting season was lower than the survival rates reported by other studies, even where hunting influenced the survival of waterfowl, for example, mallards (0.76 in Fleskes *et al*., 2010; 0.39–0.62 in Yetter *et al*., 2018; 0.57 in Palumbo *et al*., 2022) and northern pintails *Anas acuta* (0.76–0.93 in Fleskes *et al*., 2007) in North America. This issue requires further investigation with additional data.

Illegal shooting and hunting normative

The interaction between local hunting practices and the behaviour of marbled teals released by the reinforcement programme could explain the high mortality rates detected. On one hand, the use of baits (seeds, cereals) to attract game waterfowl species to hunting grounds and the habituation of the released individuals to these resources, promotes intensive use of hunting grounds by the captive-bred birds and increases the probability of their illegal killing (e.g. see movements of GPS-tagged marbled teals in Appendix S5). In addition, the fact that this species is quite cryptic and similar to other species (e.g. female red-crested pochard *Netta rufina*), coupled with the legal authorisation to hunt waterbirds in periods of reduced or no visibility (1.5 h after dusk and before dawn), unavoidably leads to deaths of non-game species. Night hunting of waterfowl could contravene European legislation which prohibits non-selective hunting methods or indiscriminate capture or killing methods, in both the Birds and the Habitats Directives (Council Directives 79/409/EEC and 92/43/EEC respectively). This is in line with recent European Court rulings (e.g. Court of Justice of the European Union, 2021). Consequently, night-time waterfowl hunting should be forbidden in Spain, as it does not meet the selectivity criterion of European legislation and accidental killings of marbled teals may affect a substantial part of the population of this endangered waterbird.

The absence of knowledge of the migratory patterns of the species, and their timing in particular, can lead to a mismatch between the establishment of the hunting season and the protection of the species. From September to November, many marbled teals are still present in Iberian wetlands. Therefore, opening the hunting season before these birds have started their migration increases their mortality risk. Obviously, there must be increased vigilance both on hunting grounds and in protected areas to prevent cases of illegal shooting and poaching, and any such incidents should be prosecuted according to the law.

Finally, although we recognise that it is necessary to reconcile traditional activities, including hunting, with conservation, it is certainly advisable not to authorise this activity in protected areas such as natural or national parks, where the main objective is the conservation of biodiversity. Wetlands are very sensitive and threatened areas (Davidson, 2014), and it is desirable to maintain areas free of hunting, especially in places where population reinforcement work is being carried out, to promote the success of conservation actions.

Reinforcement programme assessment

The reinforcement programme carried out on the studied marbled teal population has contributed to an increase in the breeding population during the recent years. However, this increase seems to be exclusively due to the way the releases are carried out, releasing 2nd cy birds and once the hunting season is over (late winter, early spring). Marbled teals can breed at 1 year of age, therefore such birds could be fit for breeding which could artificially boost the number of breeding pairs. The strategy of delaying the release of captive-bred birds until the end of the hunting season, which is logically intended to increase survival, could have the opposite effect long-term, as noted by Green *et al*. (2005). This is also supported by our population viability analyses, which indicated that the released individuals were not able to compensate for the mortality rates, and therefore the success of the reinforcement programme is dependent on the continued release of captive-bred birds.

Delaying release is likely to also have consequences for the behaviour of marbled teals. Increasing the time spent in captivity may increase reinforcement programme failure by increasing habituation to humans, loss of anti-predator behaviours or dependence on predictable food sources (Seddon, Armstrong, & Maloney, 2007; Bubac *et al*., 2019; Rowell, Magrath, & Magrath, 2020). In fact, one of the most significant problems in translocation programmes is the loss of anti-predator behaviour, which has a major impact on the survival rates of released individuals (Bubac *et al*., 2019). Animals reared in the absence of predators can lose anti-predator behaviours after just a few generations (McPhee, 2004). Therefore, reducing the residing time of marbled teals in captivity and including training to recover their anti-predator and anti-human behaviour could be good measures to increase the success of this programme.

Recommendations for future conservation actions

The critical situation of the marbled teal requires a re-evaluation of conservation strategies. The investment of around 10 M € from European LIFE projects (https://webgate.ec.europa.eu/life/publicWebsite/index.cfm) in ex situ conservation actions without mitigating the causes that led to or contributed to the species' regression, would be unwise. To establish a self-sustaining population, it is currently not enough to reinforce the population; it is necessary to reduce non-natural mortality by at least 40%. The most immediate concern is the reduction of hunting accidents and illegal shooting mortality, but actions should also be taken regarding other causes of mortality, such as controlling the presence of free-ranging cats, especially in those wetlands that are more anthropised (Lepczyk *et al*., 2022), and improving water management to prevent or minimise epizootic outbreaks (Friend, McLean, & Dein, 2001; Vidal *et al*., 2013; Anza *et al*., 2014). In addition, some improvements can be included in the reinforcement programmes, such as earlier release times or incorporating anti-predator training (Bubac *et al*., 2019).

GPS-tracking of marbled teals has confirmed the interconnection of the Iberian populations with North Africa (Carboneras & Kirwan, 2020), but further research on these migratory processes is needed to understand how the European population depends on the conservation status of the North African wetlands and the threats they face over there (Davidson, 2014). It would also be interesting to assess the effect of GPS-tracking devices on individuals. All these aspects would seem to have relevant implications for the success of conservation actions, including translocations.

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Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Ethics

The corresponding authorisations for the capture and tagging of marbled teals were provided by the 'Dirección General de Medio Natural y de Evaluación Ambiental' of the Generalitat Valenciana with the number of expedient 10SVVS/2021/201/E. s.

Authors contributions

JMPG and FB: Conceptualisation, Methodology, Investigation. JMPG, ASA and RCRC: Formal analysis. JMPG and FB: Writing—original draft. All authors: Writing review and editing.

Data availability statement

This research utilised census data collected by Generalitat Valenciana and publicly available in https://bdb.gva.es/es/censos-d-aus-aquatique. The original telemetry data set is available by request to the authors (Movebank ID 491401709).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Clutch size frequency of marbled teal *Marmaronetta angustirrostris* in wetlands of the South-Eastern Iberian Peninsula recorded during 2015–2021 field monitoring.

Figure S2. Age at death (years) of marbled teal *Marmaronetta angustirrostris* recorded from ring recoveries in wetlands of the South-Eastern Iberian Peninsula.

Figure S3. Spatial locations of recovered dead marbled teals *Marmaronetta angustirrostris* or their transmitters and unexpectedly stopped transmitters.

Figure S4. Variation of extinction probability according to adult survival for marbled teals. The extinction probability was calculated according to 100 simulations where all other parameters were held constant and only adult survival varied.

Figure S5. Movements performed by the 42 GPS-tagged marbled teals *Marmaronetta angustirrostris* in South-Eastern Spain. We show the locations of protected areas (blue line), hunting grounds (red) and GPS-trajectories (black line—transparency 20%).

Table S1. Detailed characteristics of 42 GPS-tagged marbled teal *Marmaronetta angustirrostris* in South-Eastern Spain from 2018 to 2020. Illegal Shooting Evidence indicates if transmitters unexpectedly stopped inside a hunting ground (place) or on a hunting day (date).

Table S2. Data to develop the matrix population models of marbled teals *Marmaronetta angustirrostris* in South-Eastern Spanish population.