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Survival probabilities of wintering Eurasian Woodcocks *Scolopax rusticola* in northern Spain reveal a direct link with hunting regimes

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Abstract

The management of game species relies on robust estimates of hunting-related mortality. A relative measure of this mortality can be obtained by comparing survival estimates of animals across similar areas with different hunting pressures. We conducted live recapture-dead recovery analyses on wintering Eurasian Woodcocks *Scolopax rusticola* (hereinafter "Woodcock") in provinces of Gipuzkoa (GIP) and Álava (ALA), two neighboring regions of northern Spain. The two regions have a similar number of hunting licences issued on a per day basis, but while hunting is limited to 3 days per week in ALA, in GIP it is allowed on a daily basis, resulting in a ca. 50% longer period of exposure of game species to hunting-related mortality here. We used a model based on monthly survival estimates to test whether the mortality of Woodcock varied between the two regions. Mean (\pm SE from a time-constant model) annual survival of Woodcocks was estimated to be 0.37 (\pm 0.04) and 0.56 (\pm 0.04) in GIP and ALA, respectively. If we assumed that this difference was only due to the longer period of exposure to hunting, mortality was increased by ca. 10% per additional day of hunting per week. Moreover, we also found that survival was positively associated with temperature in one of the study zones (ALA), suggesting that a high hunting pressure can override the effect of climate-dependent fluctuations. However, further research into fecundity and dispersal is necessary to assess the viability and sustainability of the wintering Woodcock populations under the current hunting regimes in these two zones.

Keywords Europe · Forest-dwelling shorebirds · Migrant game species · Hunting pressure · Population dynamics · Ringing

Zusammenfassung

Überlebenswahrscheinlichkeiten von überwinternden Waldschnepfen in Nordspanien weisen eine direkte Verbindung zu den Jagdregelungen auf

Das Management von Wildtieren ist auf verlässliche Schätzungen der durch Jagd bedingten Mortalität angewiesen. Ein relatives Maß dieser Mortalität kann man erhalten, indem man die Überlebensraten von Tieren in ähnlichen Gebieten mit unterschiedlichem Jagddruck vergleicht. Wir führten Wiederfang-Totfund-Analysen an überwinternden Waldschnepfen *Scolopax rusticola* in den Provinzen Gipuzkoa und Álava durch, zwei Nachbarregionen in Nordspanien. Diese zwei Regionen haben eine ähnliche Anzahl an Jagdlizenzen pro Tag. Während jedoch in Álava die Jagd auf nur drei Tage pro Woche begrenzt war, durfte in Gipuzkoa täglich gejagt werden, was einem 50% längeren Jagdzeitraum entspricht. Wir verwendeten ein Model basierend auf den monatlichen Überlebenswahrscheinlichkeiten, um zu testen, ob die Mortalität zwischen den beiden Regionen variierte. Die mittlere jährliche Überlebensrate der Waldschnepfe (Mittelwert ± Standardfehler aus einem Zeitkonstantenmodell) wurde auf 0.37 (±0.04) in Gipuzkkoa und 0.56 (±0.04) in Álava geschätzt. Wenn wir davon ausgehen, dass dieser Unterschied ausschließlich aufgrund des längeren Jagdzeitraums zustande kam, steigt in einer Woche die Mortalität um ca. 10% pro zusätzlichen Jagd-Tag. Weiterhin fanden wir heraus, dass die Überlebensrate positiv mit der Temperatur in einer der Untersuchungsgebiete (Álava) zusammenhing, was vermuten lässt, dass ein hoher Jagddruck den Effekt klimabedingter Schwankungen überdecken kann. Jedoch sind weitere Untersuchungen hinsichtlich Fekundität und

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Verbreitung nötig, um die Tragfähigkeit und Nachhaltigkeit der derzeitigen Jagdregelungen bezüglich der überwinternden Waldschnepfenpopulationen in diesen beiden Gebieten zu beurteilen.

Introduction

Estimates of survival probability and harvesting pressure are crucial for the sustainable management of game species (Williams et al. 2002; Duriez et al. 2005a; Robinson et al. 2008; Newton 2013). For long- and medium-distance migratory species, these data are likely to vary because hunting pressure and laws regulating hunting change throughout these species' distributions. In Europe, hunting regulations vary substantially between regions and even within a single country (Hirschfeld and Heyd 2005). The spatial scale of the problem, the lack of detailed information and the heterogeneity of hunting pressure prevent the effective management of migratory game species. The case of the Eurasian Woodcock Scolopax rusticola (hereinafter "Woodcock") is a good example of these difficulties. This species, which is a partial migrant, breeds in boreal and temperate forested habitats, from Portugal to east Asia, and in some sub-tropical Atlantic archipelagos in Macaronesia (Cramp and Simmons 1983; Machado et al. 2008). The birds in northern countries are migratory, while those at southern latitudes tend to be resident (Cramp and Simmons 1983). During the winter, southern European countries host the majority, if not all, of the European population and part of the northern Asiatic one (Hoodless 1995; Onrubia 2012).

In Europe, the species has been declining (Tucker and Heath 2004), but the relative roles of habitat change, climate change, and hunting pressure in this decline are not fully understood, with all three factors known to play a role (Fuller et al. 2007; Tavecchia et al. 2002; Duriez et al. 2005a; Péron et al. 2012). About 3-4 million birds are shot in Europe every year, essentially during the winter in western and southern Europe (Ferrand and Gossmann 2001; Hirschfeld and Heyd 2005), but also during the breeding period in north-eastern European countries. Woodcock survival estimates are not available for the whole distribution range of the species. Most survival studies have been carried out on wintering birds in France (Tavecchia et al. 2002; Péron et al. 2011a, b), but some information is also available for the UK (Hoodless and Coulson 1994), Italy (Aradis et al. 2008) and Spain (Guzmán et al. 2017). Besides hunting, survival is affected by other extrinsic sources of mortality, such as predation [accounting for 10.2% of the birds found dead (Duriez et al. 2005a)] and winter severity, which in some years can cause an additional 10% increase in the probability of mortality (Tavecchia et al. 2002).

Despite the Iberian Peninsula being one of the main wintering regions for the species in Europe (Onrubia 2012), the impact of hunting there is still poorly known (Guzmán 2013). Migratory Woodcocks wintering in the Iberian Peninsula mainly breed within the Circum-Baltic region (Hobson et al. 2013) up to Central Siberia (Guzmán et al. 2011; Hobson et al. 2013; Arizaga et al. 2014). These birds are thought to originate from different populations from those wintering in France or other areas (Arizaga et al. 2014), and robust estimates of survival probabilities are not yet available. In Spain, Guzmán (2013) observed that 36% of radio-tagged birds died within the first winter, and found a negative association between survival and temperature and between survival and predator density. Ring-recovery data analysis indicated that hunting pressure did not influence survival, which could be taken to suggest that most hunting-related mortality is compensatory (Guzmán 2013). But more recent analyses in Guzmán et al. (2017) show a clear relationship between survival and hunting pressure.

Disentangling hunting-related mortality from other causes of mortality is notoriously difficult without appropriate experiments (but see Servanty et al. 2010; Péron et al. 2012). Insights on hunting-related mortality can be obtained by comparing data from zones with contrasting hunting activity or pressure. Péron et al. (2012) found that survival in zones with low hunting pressure was 17% higher than where the hunting pressure was high (Péron et al. 2012). There is also an additional challenge in estimating the survival of wintering game species from recovery data: because banding seasons coincide with hunting, birds captured and banded early in the season may have different survival than those captured and banded afterwards. Tavecchia et al. (2002) proposed a recovery model based on monthly mortality to overcome this problem. We applied this model to assess the impact of hunting pressure on apparent winter survival of Woodcock by comparing estimates from two neighboring wintering sites (provinces) in Northern Spain with similar habitat and weather conditions but contrasting hunting regimes. If hunting has an important effect, we predict a lower survival rate in the province with higher hunting pressure. Assuming that this difference is due to the hunting regime, it should be possible to relate the rate of mortality to a measure of hunting pressure.

Materials and methods

Data collection

The study was carried out in the provinces of Gipuzkoa (GIP) and Álava/Araba (ALA) in the Basque Country, northern Spain (Fig. 1). Average monthly temperatures from October to March were obtained from the Basque Meteorological Agency, for the stations of Abetxuko C-076, and Bidania C-058 (as representative of winter temperatures in ALA and GIP, respectively). GIP is within the Atlantic region while ALA is located inland with a slightly colder and drier climate than GIP (Ruiz Urrestarazu and Galdós Urrutia 2008). The main difference between the two regions is related to hunting pressure; there is no information about the hunting bag for either. Hunting is allowed from 12 October to 21 February (approximately 20 weeks; regional order 39/2015, 3/08) in both regions, but it occurs on a daily basis in GIP, whereas it is restricted to 3 days per week in ALA (Sáenz de Buruaga et al. 2012). This difference resulted in a total hunting period that was 2.3 times longer in GIP than in ALA (Table 1). A Woodcock banding program was conducted from winter 2009 to spring 2014, i.e., from October to March (Arizaga et al. 2014). For simplicity, we will refer to all capture sessions between October of year *i* to March of year i + 1 as occurring in year *i*. Birds were caught at night, using a 12-V 100-W lamp attached to a helmet and a large circular net on 6-m-long pole (Ferrand and Gossmann 1988). Unmarked birds were equipped with a metal ring with a unique alphanumeric code. We ringed 1456 Woodcocks, about half (45%) in ALA and half (55%) in GIP (Table 2). We gathered data from 2009 to 2015 for a total of 150 live recaptures (64 individuals) and 290 Table 1 Number of hunting GIP Year ALA licences granted by the authorities in Álava (ALA) and 2009 7557 18.953 Gipuzkoa (GIP), and total days 2010 7816 18,583 7759 2011 18,202 2012 7669 17,834 2013 7759 17,263 2014 7623 NA 135 138 L/days HD 57 132 Note that hunting licences are not exclusively for Woodcock hunting L/days Average number of

licences per day of hunting, NA data not available

recoveries of dead individuals of these marked birds. Of the birds recovered dead, 98% were birds that had been shot, while for six (2%) the cause of death was unknown.

Data modeling

of hunting (HD)

Recoveries and live observations obtained during the 6 years of the study were coded into individual capture histories. Animals were sorted into six groups according to the month of first release (October, November, December, January, February and March, respectively) and the wintering zone (GIP vs. ALA). This corresponded to a total of 12 groups of birds (6×2) . We used Burnham's model in software MARK 8.0 (White and Burnham 1999) to estimate monthly survival (S), recapture probability (p) and reporting rate (r). The model includes a parameter, F, defined as the probability of birds staying in or returning to the zone of marking, based on the ratio between two survival estimates, one based on

Fig. 1 Localization and surface area (km²) of the two adjacent study zones [Gipuzkoa (GIP), Álava (ALA); shaded areas] in the Basque Country (inset), northern Spain



Table 2Number of EurasianWoodcocks (hereinafter"Woodcock") captured,recaptured (bird seen alive;L) and recovered (ringed birdreported dead; D) in the twostudy zones (with GIP havinga higher hunting pressure ascompared to ALA)

Ringed in				Recaptured in				
				ALA		GIP		
Year	ALA	GIP	State	That winter	Next winter(s)	That winter	Next winter(s)	
2009	137	123	L	_	16	_	0	
			D	4	21	8	20	
2010	77	100	L	_	3	_	2	
			D	10	8	16	6	
2011	62	201	L	_	5	_	3	
			D	5	8	18	18	
2012	174	170	L	_	12	_	10	
			D	14	23	20	18	
2013	113	154	L	_	15	_	2	
			D	13	9	22	18	
2014	97	48	L	_	_	_	-	
			D	6	_	5	_	

Data were obtained from October to March, so, for example, data for 2009 refer to those birds captured, recaptured or recovered from October 2009 to March 2010

Table 3Survival during thefirst year after marking as afunction of the month of release(October–March)

Birds released in					
October	S ^{11.5}				
November	$S^{10.5}$				
December	S ^{9.5}				
January	S ^{8.5}				
February	S ^{7.5}				
March	S ^{6.5}				

S Monthly survival

recaptures near the study area and the other based on recoveries from any part of the species distribution. As observations and recoveries used here are mainly for the study area, F has been fixed to 1.00. The survival probability during the first year after release is expected to be a function of the length of the interval, which changes according to the month of release. To accommodate this difference, we expressed the model in terms of S. Assuming S is constant throughout the year, the annual survival is equal to S^{12} . Hence, the annual survival during the first interval after marking for birds released in October was $S^{11.5}$ (note that we assumed that all birds were released in the middle of the month). This parameter was $S^{10.5}$ for Woodcocks released in November, $S^{9.5}$ for those released in December, etc. (Table 3). A loglink function was used to link survival rates of the different groups by a linear constraint $[\log(S) = \beta X$, where X is the length of the interval (see also Tavecchia et al. 2001, 2002)]. A capture-mark-recapture-recovery analysis typically begins by assessing the goodness of fit of a general model in which all parameters vary over time and to which all subsequent models are compared. The available software, such as MARK (White and Burnham 1999) and U CARE (Choquet et al. 2009), provide two options for the assessment of the goodness of fit of a general model. The first, based on contingency tables, assesses the adequacy of full time-dependent models, while the second option is based on a bootstrap technique and can be used to assess the adequacy of any model. A test of a full time-dependent model based on dead-alive encounters in software U_CARE was not significant, indicating that such a model would fit the data adequately (results not shown). However, this model appeared over-parameterized and did not include the structural link between the groups. The log-link function allowed us to linearize the differences in the first survival estimate after marking between the six groups of release; however, numerical problems can arise during the optimization of the likelihood function because it is not constrained between 0 and 1, as e.g., a logit-link function would. In our study, a general model in which S, p, and r varied according to the year, the zone and their statistical interactions did not converge. As a consequence, we assessed the goodness of fit of a simpler model. To do this we separated observations of live birds from dead birds and, in both datasets, considered a model in which p and r were assumed to vary across the zones and between years, while survival was assumed to vary only across the zones, i.e., to be constant over time. The goodness of fit of this model was assessed using a bootstrap procedure with 1000 simulations in program MARK (White and Burnham 1999). This model explained both datasets adequately (p=0.412 and p=0.385), for recovery and recaptures, respectively) and it was considered as a starting point for the analysis. Note that more complex models with additional effects on survival are also expected to fit the data due to their greater complexity. We assessed the importance of time, (t in model notation), and wintering region/zone (z, for

each parameter) and considered winter average temperature as a covariate (Temp in model notation) (Gossmann and Ferrand 2000; Tavecchia et al. 2002). Models were compared using Akaike's information criterion corrected for sample size (AICc) (Burnham and Anderson 1998). Models with Δ AICc < 2 were arbitrarily considered to fit the data equally well (Burnham and Anderson 1998).

Results

We began the analysis by simplifying the structure of the general model $[S(z)p(z \times t)r(z \times t); \text{ model 1; Table 4})$. Parameters *p* and *r* changed through time, but a difference between the two regions was only retained in *p* (model 4; Table 4). The AICc values showed that models supporting the hypothesis that survival varied between the two studied regions were better than those assuming constant survival (e.g., model 4 vs. model 11; Table 4). According to model 4, annual survival (\pm SE) was higher in ALA (0.56 \pm 0.04) than in GIP (0.37 ± 0.04) . Yearly variations of survival were weak, with temperature during the winter being positively correlated with survival in ALA [analysis of deviance (ANODEV): $F_{1,5} = 18.71$, p = 0.012], but not in GIP (ANODEV: $F_{1.5} = 0.418$, p = 0.553). Model 12, assuming an effect of temperature only in ALA, was the one with the lowest AICc value. However, the AICc value of model 4 differed by less than 2 points from model 12, hence both these models explained the data similarly well. This was due to the fact that the fluctuations in estimated survival rate between years were weak (Fig. 2). After re-assessing the influence of year on p and r, none of the subsequent models (models 15 and 16) improved the AICc values (see model ranking in Table 4). p was higher in ALA than in GIP $(0.08 \pm 0.01 \text{ and } 0.03 \pm 0.01, \text{ respectively})$ and varied over time. Similarly, r varied between years, with values ranging between 0.11 ± 0.03 and 0.29 ± 0.04 (Fig. 2). The top-ranked models showed increasing values of r throughout the study period (Fig. 3), without differences between the two zones (model 12 vs. model 15; Table 4).

Table 4Modeling monthlysurvival probability (S),recapture probability (p) andreporting rate (r) of Woodcockswintering in Northern Spain

Model	Notation	AICc	ΔAICc	wAICc	np	Deviance
12	$S(z \times \text{Temp.})^{a} p(z \times t) r(t)$	2607.86	0.00	0.36	18	386.34
4	$S(z)p(t \times z)r(t)$	2607.92	0.07	0.35	17	388.46
2	$S(z)p(t \times z)r(t+z)$	2609.97	2.11	0.13	18	388.45
13	$S(z \times \text{Temp.})p(t \times z)r(t)$	2611.75	3.89	0.05	20	386.13
14	$S(z \times \text{Temp.})^{b} p(z \times t) r(t)$	2611.85	4.00	0.05	18	388.29
10	S(t+z)p(t+z)r(t+z)	2613.08	5.22	0.03	22	383.35
15	$S(z \times \text{Temp.})^{a} p(z \times t) r$	2614.37	6.51	0.01	13	403.07
7	$S(t \times z)^{c} p(z \times t) r(t)$	2615.62	7.77	0.01	22	385.89
6	$S(z)p(z \times t)^{c}r(t)$	2616.23	8.37	0.01	14	402.89
8	$S(z \times t)^{d} p(z \times t) r(t)$	2616.41	8.55	0.01	22	386.68
9	$S(z)p(z \times t)r(z)$	2618.67	10.82	0.00	13	407.37
1	$S(z)p(t \times z)r(t \times z)$	2618.88	11.02	0.00	23	387.08
11	$Sp(t \times z)r(t)$	2619.96	12.10	0.00	16	402.54
3	S(z)p(t+z)r(t+z)	2623.49	15.63	0.00	15	408.11
16	$S(z \times \text{Temp.})^{a} p(z) r(t)$	2624.55	16.69	0.00	11	417.32
5	S(z)p(z)r(t)	2629.59	21.73	0.00	10	424.39
17	$S(z)p(t \times z)r(t \times z)^{\rm e}$	2647.01	39.22	0.00	23	415.27

Models are ranked according to their Akaike information criterion corrected for small sample size (AICc). We considered either additive models (+) or models with interactions (×). Note that site fidelity was forced to be 1 in all the models

 $\Delta AICc$ AIC difference when compared with the lowest AICc value, *wAICc* AICc relative weight, *np* number of estimable parameters in the model, *Dev* model deviance

z zone (ALA vs. GIP), t year (this parameter has different values depending on the year), *Temp*. yearly average winter temperature

^aTemp only in ALA

^bTemp. only in GIP

^ct only in ALA

 ^{d}t only in GIP

^eAll animals assumed to be released in October



Fig. 2 Survival estimates of Woodcocks released in October in each wintering zone (estimates obtained from model 7 for GIP and model 16 for ALA, Table 4). *Bars* indicate SEs. Dotted lines indicate expected value from a model assuming a relationship between the average winter temperature and survival (model 14; Table 4); this relationship was statistically significant for ALA only



Fig. 3 Reporting rate for a specific winter (e.g., 09/10 refers to the probability of a ring being reported in the winter between October 2009 and March 2010). Estimates obtained from model 4 (Table 4)

Discussion

We compared survival probabilities of wintering Woodcocks between two neighbouring regions (provinces) with contrasting hunting regimes. We found that mortality was about a third higher where hunting was allowed on a daily basis (GIP) compared with that in a zone in which it was only permitted 3 days/week (ALA). Assuming that the difference in mortality was due to the longer hunting period in GIP, we can estimate that the relative increase in mortality due to a single additional day of hunting per week is approximately 10%. At first this seems a strong assumption as the total number of hunting licences granted is higher in GIP than in ALA (Table 1); however, the number of licences granted on a per day basis is similar in the two regions (~ 136). Climatic conditions are unlikely to be responsible for the 33% increase in mortality found in GIP. Indeed, winters are generally milder here than in other Woodcock wintering areas, and the difference between average temperatures between the two provinces is only 1–2 °C. Péron et al. (2011b) studied the association between overwintering survival and winter conditions and found that even during cold spells differences in survival values were not as large as the one found here. Moreover, the average winter temperature was lower in ALA, where survival was found to be higher.

With the information available at present, differences in survival probabilities between the two localities can only be ascribed to the longer hunting period in GIP, which results in a longer exposure to hunting-related mortality. This conclusion is also in agreement with evidence from other studies. High levels of hunting-related mortality during the winter resulted in a decreasing Woodcock population at wintering quarters in central Italy and France (Aradis et al. 2008; Péron et al. 2011a, 2012). These authors noted that first-year Woodcocks tended to occupy zones with lower densities of birds, hence compensating to some extent for the mortality of adults in preceding winters in a source-sink dynamic. The difference between survival estimates might be due to a surplus of young (first-year birds) in GIP compared to ALA. Although theoretically possible, this explanation seems unlikely. A different age ratio would hardly result in a difference of 34% in survival estimates unless the hypothesis included a complete age-dependent separation between the birds. Duriez et al. (2005b) did not find any effect of age on Woodcock wintering behaviour; thus, according to this finding, a similar age ratio would be expected in the two areas in our study. Yet, the average annual survival in GIP (0.37) was similar to, or lower than, those for first-year birds reported in France [0.34 (Tavecchia et al. 2002); 0.47 and 0.33 for juveniles in areas with low and high hunting pressure, respectively (Péron et al. 2012)] and in the UK (Hoodless and Coulson 1994) and the lowest value registered so far in Europe.

Tavecchia et al. (2002) made an attempt to estimate the value of survival needed to sustain a hypothetical Woodcock population. They found that an adult survival probability of 0.44 and a first-year survival of 0.34 were not sufficient to maintain a stable population, which would indicate that the population in GIP is decreasing or acting as a demographic sink (Pulliam 1988). Our estimates of survival in ALA and GIP were also below the average estimates reported in zones without hunting activity (Duriez et al. 2005a), suggesting that hunting pressure is the main cause for the spatial differences between them (Péron et al. 2012). Moreover, estimates for GIP are lower than those found in France (Tavecchia et al. 2002), even when compared to regions with high hunting pressure (Péron et al. 2012), or in Spain (Guzmán 2013). Winter survival of Woodcock is also influenced by winter

severity (Tavecchia et al. 2002). Despite neither of the two zones showing important yearly variation in survival or average winter temperature, winter temperature was positively related to survival in ALA but not in GIP. Tavecchia et al. (2002) found that the strength of the relationship between winter temperature and survival increased with latitude. In our study, the change in mortality could hardly be considered to correspond to the small difference in temperature between the two zones. More importantly, and contradicting predictions, the highest survival was found in ALA, the zone with the lowest temperatures. On the other hand, given the small difference between the average temperatures, we wondered why the influence of winter severity was not retained in GIP. It is possible that the high level of hunting-related mortality here buffers the influence of temperature. This is currently only speculative, and additional data are needed to further explore this.

Finally, we observed an increase in the reporting rate during the study period, with the mean value ranging from 0.10 at the beginning to 0.28 at the end of the study. As the number of hunters did not increase during this period (Table 1), this result suggests an increase in public awareness or an improvement in communication of the campaign. Following Tavecchia et al. (2001, 2002) we used a model based on monthly survival to overcome the problem generated by conducting ringing of the birds during the hunting season. When mortality occurs during marking, survival probabilities are generally overestimated because birds marked early in the season have lower survival than those marked later. For example, survival estimates derived from a model in which all Woodcock were erroneously assumed to be released in October were ~ 17% higher (0.62 and 0.45 in ALA and GIP, respectively) than those obtained by accounting for the month of release. The AICc of this 'incorrect' model was approximately 40 points higher than that of the model considering the month of release for each bird (model 17 vs. model 1; Table 4).

In conclusion, the annual survival of Woodcocks wintering in two nearby zones in northern Spain varied with hunting pressure. Our data suggested a mortality increase of about 10% for every additional day of hunting per week. Given the current hunting pressure in GIP and the direct link between mortality and hunting days, as suggested by the comparison with Woodcock survival in ALA, there seems to be no allowance for a compensatory response in this former province. To our knowledge this is the first study that has attempted to relate mortality to a measure of daily hunting pressure. As the data indicate that mortality is related to the number of hunting days, one possibility is to experimentally change the hunting pressure to disentangle natural from hunting-related mortality. For example, assuming all mortality is additive, a decrease of ~ 10% in relative mortality per day of hunting would lead to a natural survival rate of 0.74.

Further research should evaluate the level of sustainable hunting pressure by integrating data with regards to time of survey, fertility and site fidelity with those presented here.

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