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Demographic and evolutionary consequences of hunting of wild birds

Emilienne Grzegorzczak¹, Alain Caizergues², Cyril Eraud³, Charlotte Francesiaz⁴,
Kévin Le Rest² and Matthieu Guillemain^{5,*} 

¹Office Français de la Biodiversité, Service Conservation et Gestion Durable des Espèces Exploitées, 405 Route de Prissé-la-Charrière, Villiers-en-Bois 79360, France

²Office Français de la Biodiversité, Service Conservation et Gestion Durable des Espèces Exploitées, 08 Bd A. Einstein, CS42355, Nantes Cedex 3 44323, France

³Office Français de la Biodiversité, Service Conservation et Gestion des Espèces à Enjeux, 405 Route de Prissé-la-Charrière, Villiers-en-Bois 79360, France

⁴Office Français de la Biodiversité, Service Conservation et Gestion Durable des Espèces Exploitées, 147 Avenue de Lodève, Juignac 34990, France

⁵Office Français de la Biodiversité, Service Conservation et Gestion Durable des Espèces Exploitées, La Tour du Valat, Le Sambuc, Arles 13200, France

ABSTRACT

Hunting has a long tradition in human evolutionary history and remains a common leisure activity or an important source of food. Herein, we first briefly review the literature on the demographic consequences of hunting and associated analytical methods. We then address the question of potential selective hunting and its possible genetic/evolutionary consequences. Birds have historically been popular models for demographic studies, and the huge amount of census and ringing data accumulated over the last century has paved the way for research about the demographic effects of harvesting. By contrast, the literature on the evolutionary consequences of harvesting is dominated by studies on mammals (especially ungulates) and fish. In these taxa, individuals selected for harvest often have particular traits such as large body size or extravagant secondary sexual characters (e.g. antlers, horns, etc.). Our review shows that targeting individuals according to such genetically heritable traits can exert strong selective pressures and alter the evolutionary trajectory of populations for these or correlated traits. Studies focusing on the evolutionary consequences of hunting in birds are extremely rare, likely because birds within populations appear much more similar, and do not display individual differences to the same extent as many mammals and fishes. Nevertheless, even without conscious choice by hunters, there remains the potential for selection through hunting in birds, for example by genetically inherited traits such as personality or pace-of-life. We emphasise that because so many bird species experience high hunting pressure, the possible selective effect of harvest in birds and its evolutionary consequences deserves far more attention, and that hunting may be one major driver of bird evolutionary trajectories that should be carefully considered in wildlife management schemes.

Key words: birds, density dependence, harvesting, selection, plasticity, wildlife management.

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* Author for correspondence (Tel.: +33 4 90 97 28 79; E-mail: matthieu.guillemain@ofb.gouv.fr).

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I. INTRODUCTION

Wildlife harvesting has a long tradition in human lineages including *Homo neanderthalensis* and *H. sapiens* (Sykes, 2022). Although still a matter of debate, numerous studies suggest that prehistoric humans had a tremendous impact on wildlife communities and greatly increased extinction rates through hunting, especially in birds (Duncan, Blackburn & Worthy, 2002; Broughton, 2004; Bovy, 2007; Cooke *et al.*, 2023). Evidence of bird hunting throughout more recent human history is recorded from Ancient Egypt (Bailleul-LeSuer, 2012), during the Iron age (Best & Mulville, 2016), in Ancient Greece and Rome (Åkerström-Hougen, 1976; Trinquier & Vendries, 2009), as well as throughout the Middle Ages and Renaissance (Anderson, 1985; Albarella & Thomas, 2002; Gorobets & Kovalchuk, 2017; Corbino & Albarella, 2019). Whether for subsistence or leisure, hunting has taken place on all continents, in all territories occupied by humans through time, and subsistence hunting persists across indigenous cultures to the present day (IPBES, 2022). Hunting, together with other factors such as habitat change, has been the direct cause of extinction of tens of bird species in Pacific islands (Milberg & Tyrberg, 1993; Duncan *et al.*, 2002). The most famous example of such human-caused extinction of native birds is that of the moas (order Dinornithiformes), giant birds of New Zealand decimated soon after the arrival of Polynesians *ca.* 1300 CE (Anderson, 1989; Holdaway & Jacomb, 2000; Allentoft *et al.*, 2014). Overharvesting, alone or in combination with other types of human-related pressures, also caused disappearance of the dodo (*Raphus cucullatus*) on Mauritius, the great auk (*Pinguinus impennis*) in the North Atlantic, and the passenger pigeon (*Ectopistes migratorius*) and Carolina parakeet (*Conuropsis carolinensis*) in North America (Bengtson, 1984; Fuller, 2003; Jackson & Jackson, 2007; Guiry *et al.*, 2020). During the 18th and 19th centuries, commercial bird hunting arose to meet demands for meat for consumption and feathers for fashion hats, with millions of individuals harvested locally or imported annually in England and the USA alone for the millinery fashion industry (Doughty, 1972) and meat trade (Smalley & Reeves, 2022). Since then, commercial hunting has declined both in Europe and North America, but leisure hunting remains a common hobby in many parts of the world [e.g. France (Aubry *et al.*, 2016); Europe (Hirschfeld, Attard & Scott, 2019); North America (Raftovich *et al.*, 2021)]. Since the rise of the genus *Homo* and perhaps before, bird hunting has been widely practised and is potentially harming wild populations already under

pressure from rapid environmental changes and other anthropogenic mortality sources (Loss, Will & Marra, 2015; IPBES, 2022).

An awareness that bird populations, long considered infinite, were becoming depleted led to calls to regulate harvest through dedicated management in the early 20th century (Organ *et al.*, 2012; Bastmeijer, 2016). This problem was particularly acute in North America, where the first law banning spring hunting, migratory bird trade, and the import of wild bird feathers was passed in 1913 (the Weeks–McLean Act). Subsequently, the Migratory Bird Treaty Act of 1918 represented the first international agreement (initially between the USA and Canada, with Mexico, Japan, and Russia joining later) aimed at the conservation of migratory birds at flyway scale (<https://www.fws.gov/history-of-fws>). Since then, a number of treaties and acts have been passed in the USA to make bird harvesting sustainable; the most recent and ambitious being the North American Waterfowl Management Plan (Cooch *et al.*, 2014; Anderson *et al.*, 2018, see <https://nawmp.org/>). In Europe, instead of targeting hunting, the first law concerning bird conservation was aimed at protecting birds considered to be useful to economic activities, such as passerines, storks or woodpeckers, which consume insects that are pests of agriculture or forestry. This seminal international agreement, the Convention for the Protection of Birds Useful to Agriculture, was adopted in Paris on 19 March 1902 by 12 European states (Bowman, 2014). Protection for a wider range of bird species was only agreed in 1950 and passed in 1962 (International Convention on the Protection of Birds, see https://www.fedlex.admin.ch/eli/cc/1955/1036_1062_1070/fr). Other laws or directives were passed in Europe subsequently, with the 2 April 1979 Birds Directive (revised in 2009, <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32009L0147>) now the overarching bird protection legislation in the EU. A large number and wide variety of laws and texts also have been passed at a national level in EU and non-EU states.

Bird hunting has a major cultural and/or economic importance in many parts of the world [see for example IPBES (2022) section A.1.2], but it is suspected to alter the demographic trajectories of populations, potentially threatening their long-term viability. Like many other taxa, birds are also under threat due to other human activities such as agriculture, habitat change, collisions with infrastructure, or predation by domestic pets (Calvert *et al.*, 2013; Loss *et al.*, 2015; Maxwell *et al.*, 2016; Jaureguiberry *et al.*, 2022). Thus, in order to reconcile apparently contradictory goals such as conservation and exploitation of natural populations,

harvest management schemes of bird populations are being implemented, under the general theoretical framework of sustainable use.

All recent laws aiming at improving bird conservation stress the need for sustainable exploitation [e.g. the 2009 revision of the European Birds Directive (<https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32009L0147>) or the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) (Madsen *et al.*, 2015)]. However, harvest levels can only be sustainable when the mechanisms underlying population dynamics, and especially the responses of bird populations to harvesting, are understood.

The consequences of harvest on the demography of wild populations have been addressed in a range of taxa including ungulates, carnivores, fish and birds (e.g. Beverton & Holt, 1993; Wright & Trippel, 2009; Servanty *et al.*, 2011; Sedinger & Herzog, 2012; Zbinden *et al.*, 2018). The first study on the impact of exploitation on fish stocks was published as early as 1900 (Garstang, 1900). Until the 1920s, demographic models remained simple and usually did not consider age or size structure to evaluate how populations were affected (Quinn, 2003). Work by Lotka (1925) on age-structured populations, followed by Leslie (1945) and Usher (1966) on matrix population models, provided insights into the effects of harvest on population growth rates. From 1980 to 2000, the rise of computational technology coupled with improvements in mathematics and statistics allowed the development of powerful and flexible modelling approaches such as non-linear models (Clark & Mangel, 1979; Logan & Allen, 1992) and those allowing the inclusion of environmental and demographic stochasticity (Mangel & Tier, 1993; Renshaw, 1993; Gyllenberg, Högnäs & Koski, 1994). The development of capture–mark–recapture (CMR) models since the 1960s made it possible to estimate fundamental demographic parameters such as annual survival, population size, and population growth rate robustly (e.g. Burnham *et al.*, 1987; Lebreton *et al.*, 1992; Pradel, 1997; Lindberg, 2012). The rise of Bayesian methods in the 2000s (Quinn, 2003; Ellison, 2004) was also a major step forward in modelling population dynamics (Kéry *et al.*, 2009; Park & Haran, 2018; for a summary of Bayesian statistics in ecology see Dorazio, 2016). One strength of the Bayesian approach is that it allows the explicit inclusion of earlier knowledge *via* the attribution of prior values. Bayesian computational approaches such as Markov Chain Monte Carlo (MCMC) allow the inclusion of independent data sources in a unique framework, e.g. building integrated population models that combine marking and census data (e.g. Gamelon *et al.*, 2021; Schaub & Kery, 2021).

For a long period, studies mostly focused on the numerical demographic consequences of hunting in terms of the size/volume of the harvest, aiming to assess whether hunting mortality was additive or compensatory to natural mortality (Anderson & Burnham, 1976; Pöysä, 2004; Sedinger *et al.*, 2010; Sedinger & Herzog, 2012; Cooch *et al.*, 2014) (see Section II). While survival rate is a key factor for predicting the demographic impact of harvesting, it is far from being

the only one. Thus, we also review other less-studied factors underlying the potential impacts of hunting mortality, such as life-history strategies, density dependence and individual heterogeneity.

Haldane (1942) was the first to highlight that besides affecting population size, harvest can lead to phenotypic selection, with various ecological and evolutionary consequences on populations depending on the phenotype (e.g. fur colour) harvested. This potential for harvest to act as a selection pressure has been studied increasingly since the 1980s, mostly in ungulates and fish, where individuals can easily be targeted and harvested according to their phenotypic characteristics, e.g. antler size in ungulates, or body length in fish (Hart & Pitcher, 1983; Kuparinen & Festa-Bianchet, 2017). The scientific consensus is that harvest can act as a selective pressure that may drive phenotypic responses in exploited populations (Allendorf & Hard, 2009; Kuparinen & Festa-Bianchet, 2017; Festa-Bianchet & Mysterud, 2018). Yet, the underlying mechanisms of these phenotypic responses, such as phenotypic plasticity or changes in genetic/genomic structure, are difficult to tease apart. Our second aim therefore is to review the possible evolutionary consequences of hunting.

Assessing the impact of harvest in birds is of interest for both conservation and society. First, a very large number of birds are harvested annually. In Europe, for example, at least 52 million birds are estimated to be shot every year [see Hirschfeld *et al.* (2019) for the years 2013–2015]. In North America *ca.* 11 million ducks, close to 3 million geese and more than 11 million mourning doves (*Zenaidura macroura*) were legally shot during the 2020 hunting season (Raftovich *et al.*, 2021). In North America, 60 bird species are subject to harvesting on a regular basis, but the Migratory Bird Treaty Act records 170 potentially huntable bird species. The Birds Directive records 65 bird species for which hunting is allowed in at least one country of the EU. Birds form a very diverse group, with a wide range of life-history trait combinations from ‘slow’ pace-of-life species (*sensu* Stearns, 1992) with high annual survival rates and low fecundity, to ‘fast’ species with high fecundity but poor survival. They have a broad range of mating systems (e.g. monogamy, polygyny, lekking) and disparate requirements in terms of habitat and ecology. Hunting practices also differ widely depending on species, regions and periods. Finally, birds currently display a wide conservation status range, from strongly declining species like the turtle dove (*Streptopelia turtur*) or black-tailed godwit (*Limosa limosa limosa*) for which hunting moratoriums have become necessary, to increasing or overabundant ones like the snow goose (*Anser caerulescens*) whose rapidly increasing numbers are causing damage to crops and nesting habitats despite very liberal hunting rules (e.g. Koons, Aubry & Rockwell, 2019). Finally, birds have been the subject of long-term censuses, ringing schemes, and sometimes dedicated hunting management programmes (e.g. Nichols *et al.*, 2007; Madsen *et al.*, 2017). Therefore, on ecological, economic, ethical and sociological grounds it is important to understand the consequences

of harvest on wild bird populations and the processes involved to allow us to improve knowledge and prioritise conservation issues.

II. THE DEMOGRAPHIC IMPACTS OF HUNTING AND THEIR POTENTIAL CONSEQUENCES ON POPULATION SIZE

(1) Exploitation and population size

The first likely consequence of exploitation is a decrease in population size (Nixon, Donohoe & Nash, 1974; Hasan, 2005; Benítez-López *et al.*, 2017). However, in early work it was difficult to tease apart the effects of harvest from those of other potential limiting factors such as changes in habitat availability/quality, climate, or predation pressure (Raveling & Heitmeyer, 1989; Peres, 2001; Wilberg *et al.*, 2011). Recent CMR modelling approaches now allow investigation of the effects of different sources of mortality on survival rates (Pollock, Conroy & Hearn, 1995; Schaub & Pradel, 2004). However, decoupling can occur between a population trend and hunting pressure (Lefebvre *et al.*, 2017; Koons *et al.*, 2019), with some species continuing to decline even after hunting is banned (Rideout *et al.*, 2015; Jolivet & Bretagnolle, 2002). In addition, hunting may have either indirect or delayed ecological consequences such as disturbance or crippling loss, reducing a population to below a level where recovery is possible, or changes in migration routes or stopover sites, which makes the evaluation of its effects on population size more complex (Mainguy *et al.*, 2002; Béchet *et al.*, 2003; Féret *et al.*, 2003).

A major goal of harvest management theory is to maximise bag size (= the number of harvested individuals) over the long term while maintaining the conservation status of

populations and supporting their ecosystem services such as recreational use [e.g. see Madsen *et al.* (2015) for waterbirds]. To enable such calculations it is essential to have the best possible understanding of the impact of hunting on survival rates (Geis & Crissey, 1969; Rolland *et al.*, 2010; Sandercock *et al.*, 2011; Prieto *et al.*, 2019).

(2) Additive versus compensatory hunting mortality

To evaluate better the impact of exploitation on population growth rates, it is important to understand how hunting interacts with natural mortality or fecundity. A range of possible interactions have been described which lie along a continuum of compensation–additivity of hunting mortality to natural mortality (Sandercock *et al.*, 2011; Péron, 2013; Fig. 1; Table 1). Full compensation (Fig. 1D) occurs when hunting and natural mortality compete entirely with one another (see Baranov, 1918), such that all harvested individuals would have died from natural causes. The evidence suggests that this is rare, with partial compensation seeming to be most common (Table 1; Fig. 1C; Burham & Anderson, 1984; Nichols *et al.*, 1984; Bartmann, White & Carpenter, 1992; Sandercock *et al.*, 2011; Péron, 2013). By contrast, additive mortality (Fig. 1A, B) occurs when the two sources of mortality combine without interacting: hunted individuals would otherwise have survived. The compensation–additivity concept is important since it is used to assess the intrinsic ability of a population to sustain a given harvest level, and should be incorporated into the design of optimal harvest strategies (Lebreton, 2005).

Several statistical approaches have been developed to assess the compensation–additivity state for hunting mortality in natural populations, often using birds as study models [e.g. Anderson & Burnham, 1976; Burnham, White & Anderson, 1984; Schaub & Lebreton, 2004; Otis &

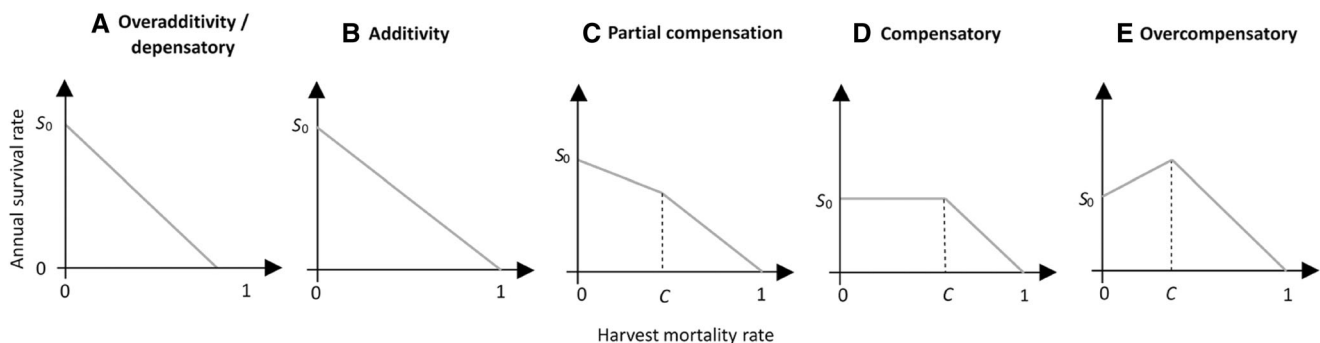


Fig. 1. Different possible additive or compensatory interactions between harvest mortality and annual survival rates (adapted from Sandercock *et al.*, 2011). S_0 is annual survival rate in the absence of hunting. Where there is an additive effect (A, B), an increase in mortality rate due to harvest leads to a decrease in annual survival rate, with this decline being steepest in the case of overadditivity (A). Partial compensation (C) occurs when part of the hunting mortality is compensated (for example by reduced mortality from other causes) and the decline in annual survival rate is therefore lower up to a threshold C . Where there is full compensation (D), hunting mortality has no impact on annual survival rate up to C . However, in both C and D when hunting mortality exceeds C , compensation no longer occurs and mortality becomes additive. (E) In the case of overcompensation, when S_0 is low, annual survival may actually increase as hunting mortality rate increases, up to threshold C beyond which the effects again become additive.

Table 1. Response of populations of insects, mammals, fish and birds to harvest and their position along the additivity–compensation gradient.

Studied species	Main result	Position along the additivity–compensation gradient	Reference
Wild boar (<i>Sus scrofa scrofa</i>)	‘The natural mortality of female wild boars increased with hunting mortality, likely as a consequence of noncontrolled mortality by crippling loss’ (p. 1922).	Overadditivity	Servanty <i>et al.</i> (2010)
Sandhill crane (<i>Grus canadensis</i>) and mourning dove (<i>Zenaidura macroura</i>)	No explanation provided by author.	Overadditivity	Péron (2013)
Black-tailed prairie dog (<i>Cynomys ludovicianus</i>)	In addition to affecting survival, hunting results in a dramatic decrease in reproductive parameters the summer following the hunting season.	(Overadditivity) Additivity	Pauli & Buskirk (2007)
Mallard (<i>Anas platyrhynchos</i>)	Hunting mortality is additive for the period 1979–1989.	Additivity	Smith & Reynolds (1992)
Canada goose (<i>Branta canadensis</i>)	The liberalisation of hunting has led to a decrease in annual survival rates of locally nesting adults.	Additivity	Iverson <i>et al.</i> (2014)
Greater snow goose (<i>Anser caerulescens atlantica</i>)	There was a significant inverse relationship between winter survival and the kill rate.	Additivity	Gauthier <i>et al.</i> (2001)
Columbian black-tailed deer (<i>Odocoileus hemionus columbianus</i>)	For ≥ 1.5 -year-old males hunting was additive as a shortened hunting season and a consequent decrease in harvest rate resulted in increased annual survival.	Additivity	Bender <i>et al.</i> (2004)
Black brant (<i>Branta bernicla nigricans</i>)	As the ring recovery rate by hunters decreased between 1950 and 2000, goose survival increased, showing that hunting mortality is additive to other sources of mortality.	Additivity	Sedinger <i>et al.</i> (2007)
Scandinavian brown bear (<i>Ursus arctos</i>)	Survival and reproduction rates decreased during periods of increased hunting pressure.	Additivity	Gosselin <i>et al.</i> (2015)
Willow ptarmigan (<i>Lagopus lagopus</i>)	Partial compensation under a 15% harvest rate and additive mortality under a 30% harvest rate. The 30% harvest rate treatment also had an effect on winter survival, which may suggest compensatory responses to this level of harvest.	Partial compensation, additivity and overadditivity	Sandercock <i>et al.</i> (2011)
Cougar (<i>Puma concolor</i>)	Two populations of cougar were studied in Utah, one heavily hunted and the other semi-protected. The hypothesis of additive mortality could not be rejected for the heavily hunted population while there was partially compensation in the other population.	Additivity and partial compensation	Wolfe <i>et al.</i> (2015)
Snow goose (<i>Anser caerulescens caerulescens</i>)	Most mortality induced by hunting was compensated by the geese during their first year. For adults, however, hunting mortality does not seem to be compensated even though the impact of hunting on survival varies according to population density and harvest dynamics.	Compensation and additivity	Calvert <i>et al.</i> (2017)
Greater sandhill crane (<i>Grus canadensis tabida</i>)	When harvest does not target specific individuals, it becomes additive when harvest rate exceeds 5%. When hunting is targeted at non-resident birds it is compensatory to natural mortality.	Compensation and additivity	Wheeler <i>et al.</i> (2021)
White stork (<i>Ciconia ciconia</i>)	Analyses showed a slight compensation of power line mortality in juveniles only; in adults, additivity or compensation of this mortality could not be tested.	Slight compensation	Schaub & Lebreton (2004)
Canada goose (<i>Branta canadensis</i>)	In non-reproductive geese, ring recovery rates by hunters were weakly positively correlated with survival rates, suggesting at least partial compensation.	Partial compensation	Iverson <i>et al.</i> (2014)

(Continues on next page)

Table 1. (Cont.)

Studied species	Main result	Position along the additivity–compensation gradient	Reference
Mallard (<i>Anas platyrhynchos</i>)	The hypothesis of total additivity was rejected.	Partial compensation	Burnham & Anderson (1984)
Red grouse (<i>Lagopus lagopus scoticus</i>) and ruffed grouse (<i>Bonasa umbellus</i>)	The degree of compensation varied according to species and age class.	Total and partial compensation	Ellison (1991)
Greater sage-grouse (<i>Centrocercus urophasianus</i>)	This study focused on two populations, one in Colorado and the other in Nevada. Although the statistical analyses had low statistical power for the Nevada population, in both cases hunting mortality does not seem to be additive.	Partial compensation	Sedinger <i>et al.</i> (2010)
Willow ptarmigan (<i>Lagopus lagopus</i>)	Overwinter rate of change in willow ptarmigan density compensated for 33% of the harvest mortality, and the compensation was density independent.	Partial compensation	Pedersen <i>et al.</i> (2004)
Mule deer (<i>Odocoileus hemionus hemionus</i>)	Density-dependent survival rates in fawns suggest a compensatory mortality process.	Compensation (at least partial)	Bartmann <i>et al.</i> (1992)
Mallard (<i>Anas platyrhynchos</i>)	‘The combined results for males, especially adults, permit rejection of the additive mortality hypothesis and point toward a highly compensatory mortality process [...]. Results for female mallards are much less conclusive [...], much of the available evidence tends to favour the compensatory mortality hypothesis’ (p. 549).	Compensation (at least partial)	Nichols <i>et al.</i> (1984)
Redhead (<i>Aythya americana</i>) and greater sage-grouse (<i>Centrocercus urophasianus</i>)	‘In Redheads, the compensation rate C was significantly lower in hatch-year birds [...] than in after hatch-year birds [...]. In sage grouse, the available information did not allow rejection of the additivity hypothesis in hatch-year birds [...] while the reverse was true in after hatch-year birds’ (p. 412).	Compensation (only in after hatch-year birds for grouse)	Péron (2013)
Bulb mite (<i>Rhizoglyphus robini</i>)	‘Harvesting adult fighters reduced the killing pressure on immature males in our experiment, which resulted in an overcompensatory number of immature fighters that matured as adults’ (p. 738).	Overcompensation	Smallegange <i>et al.</i> (2018)
Smallmouth bass (<i>Micropterus dolomieu</i>)	‘An intensive seven-year removal of adult, juvenile, and young-of-the-year smallmouth bass [...] resulted in an increase in overall population abundance, primarily due to increased abundance of immature individuals’ (p. 2279).	Overcompensation	Zipkin <i>et al.</i> (2008)

White, 2004; Sedinger *et al.*, 2010; Servanty *et al.*, 2010; Gamelon *et al.*, 2021; see reviews in Péron (2013) and Cooch *et al.* (2014)]. Studies have highlighted a variety of levels of hunting compensation depending on population or species (Sedinger *et al.*, 2010, Sandercock *et al.*, 2011), and the most recent illustrate how ecological processes can interact with anthropogenic pressures in shaping the responses of populations to harvest (Riecke *et al.*, 2022).

(3) Compensatory hunting mortality: evidence and sources of variation

Species-specific demographic traits, also called life-history strategies, are a key source of variability in the ability of a population to compensate for hunting mortality: ‘slow’

strategists with a long lifespan, late reproduction and low fecundity exhibit less compensation than ‘fast’ strategists with lower life expectancy, early reproduction and high fecundity (e.g. Péron, 2013). However, hunting may affect parameters other than survival, for instance breeding success (Mainguy *et al.*, 2002), suggesting that even ‘fast’ species whose population dynamics are driven by annual productivity might show low levels of compensation.

Density dependence also plays a central role in the ability of a population to compensate for hunting mortality, since where there is high density dependence, population size at the end of the hunting season will profoundly affect demographic parameters such as survival or reproductive rate of the remaining individuals (Both, 1998; Lebreton, 2005; Sedinger & Herzog, 2012; Woodworth *et al.*, 2017; Catlin

et al., 2019). It is difficult to predict the consequences of population density on breeding success (Lebreton, 2009), but in the classical case of a population displaying a logistic growth rate associated with a linear density dependence, the ability to compensate for harvest is considered to be maximal when population size is at half the carrying capacity, because this is when the population is most productive (e.g. see Runge, Kendall & Nichols, 2004; Lebreton, 2005).

The period when harvest occurs can also affect whether a population can compensate for hunting mortality (Kokko, 2001). Closer to the breeding period: (i) the reproductive value of an individual increases; and (ii) competition between mortality sources is relieved, so that harvest becomes less likely to be compensated by increased survival (but see how timing of harvest, density dependence and individual quality may interact in Caudill *et al.*, 2017). A similar logic can be applied to spatial processes: harvest is more likely to be compensated when it is practiced in areas where other mortality sources are more acute.

Finally, inter-individual heterogeneity for demographic traits can potentially contribute to the ability of a population to compensate for harvest. When a population is composed of individuals displaying either poor or good survival (e.g. see Kendall *et al.*, 2011; Guillemain *et al.*, 2014), targeting individuals with the lowest intrinsic survival probability will maximise compensation, a process especially studied in birds (Lindberg, Sedinger & Lebreton, 2013; Cooch *et al.*, 2014; Arnold, 2021; Riecke *et al.*, 2022). The same holds for heterogeneity in fecundity (Cooch *et al.*, 2014). Among the major avenues for future research is this question of individual heterogeneity in demographic parameters and its consequences for population trends and management, including harvest (e.g. Caudill *et al.*, 2017). Recent analytical developments now facilitate identifying the existence of different categories of individuals, even within a given age and sex class (Lindberg *et al.*, 2013; Guillemain *et al.*, 2014). Recent studies described such hidden heterogeneity in survival rate among a variety of hunted bird species in Europe and North America, recording inter-individual differences in over half of the studied cases, suggesting this is a common phenomenon (Arnold, 2021; Grzegorzczak, 2023). The next step will be to assess the drivers of such individual differences, to allow harvest management policy to be adapted. Preliminary results from Grzegorzczak (2023) could not link the probability of being a poor survivor to commonly measured indices such as body mass or folded wing length. Future investigations could assess whether some morphometric parameters are better predictors of survival rate, or if individual behaviour classes or personality traits (e.g. boldness) are good proxies for use in hunting management.

(4) The role of harvest structure on the ability to compensate for hunting mortality

All factors described in Section II.3 can modulate the ability of populations to compensate for a given volume of harvest. However, the composition of the harvest itself also plays a

role. Harvest structure, such as the share of each age or sex class in the hunting bag, can also affect the extent to which a population can compensate, if a given sex or age category contributes more to population growth (Hauser, Cooch & Lebreton, 2006). For instance, juvenile birds often have a lower reproductive value compared to adults (Nol & Smith, 1987; Forslund & Larsson, 1992; Forslund & Pärt, 1995; Blums & Clark, 2004; Baldassarre, 2014), so their harvest will affect population dynamics to a lesser extent than that of adults. Non-intentional selection of birds of a given sex or age class has been demonstrated in several hunting studies (Alford & Bolen, 1977; Giroux & Bédard, 1986; Metz & Ankney, 1991; Madsen, 2009; Christensen *et al.*, 2017). In some areas and for bird species like capercaillie (*Tetrao urogallus*) in France (Thiel *et al.*, 2007), ring-necked pheasant (*Phasianus colchicus*) in North America (e.g. Jarvis & Engbring, 1976) or common eider (*Somateria mollissima*) in Denmark (Tjørnløv *et al.*, 2019), only males can be legally hunted because females have a greater role in the population dynamics of these polygamous species, and harvesting only males preserves the potential for population growth. Harvest policy targeting males is possible owing to obvious plumage differences, and effective in terms of population conservation because a few males can fertilise many females, and males do not participate in incubation and chick rearing. Similarly to the reasoning for individual heterogeneity in demographic parameters described in Section II.3, managers should try to promote preferential harvest of the categories of individuals that contribute the least to population dynamics, and protect those which contribute the most (e.g. Caudill *et al.*, 2017).

III. THE PHENOTYPIC IMPACT OF HUNTING AND ITS POTENTIAL CONSEQUENCES ON EVOLUTIONARY TRAJECTORIES OF POPULATIONS

Because it can exert a strong selective pressure on populations, exploitation of wildlife can affect their genetic composition and hence their evolutionary trajectory (Kuparinen & Festa-Bianchet, 2017).

(1) Evidence of phenotypic changes caused by hunting and fishing

Selection through harvest is possible only if the phenotypic structure of the harvested individuals differs from that of the whole population. Many examples exist of preferential harvest of some phenotypes, the most common being related to size and/or secondary sexual characters. This is particularly true for some ungulates where hunted individuals are chosen according to their sexual attributes (antlers or horns), with hunters seeking larger trophies (Fenberg & Roy, 2008; Festa-Bianchet *et al.*, 2014; Festa-Bianchet, 2017; Büntgen *et al.*, 2018). Fishing also involves selective harvesting,

especially when net mesh size places a limit on the minimum size of individuals caught, so that only larger and older individuals are retained. In rod fishing, selection can also occur through active decisions to kill or to release individuals depending on some character, often body length, and hence can be part of a management system to maximise yield while protecting some age classes (e.g. slot limits in Gwinn *et al.*, 2015).

Beside deliberate selection by hunters or fishermen, selective harvest can also occur when some categories of individuals are more exposed to harvesting than others, without any deliberate choice by hunters or fishermen. In fish, some catching modes lead to differential harvest depending on migration and breeding phenology (Tillotson & Quinn, 2018). For example, for sockeye salmon (*Oncorhynchus nerka*) most harvest involves later migrating individuals and breeders (Quinn *et al.*, 2007). Unintentional selection may also occur due to behavioural traits (reviewed by Leclerc, Zedrosser & Pelletier, 2017): bold individuals tend to be captured more frequently with passive methods like fishing rods, traps, or standing nets, while active methods like trawling nets catch a greater proportion of shy fish (Diaz Pauli *et al.*, 2015; Arlinghaus *et al.*, 2017). In brown trout (*Salmo trutta*), individuals with more exploratory behaviour have greater exposure to fly-fishing (Härkönen *et al.*, 2014), and a similar phenomenon was recorded for the harvest of elk (*Cervus elaphus*) (Ciuti *et al.*, 2012). Whether intentional or not, harvesting by size criteria is the most common, probably because animal size is consciously or unconsciously targeted by hunters/fishermen (Beattie, 2019), and/or because it is one of the most tractable parameters.

Preferential selection for some phenotypes can gradually lead to changes in the mean population values of these traits. In mammals, trophy hunting has led to a decrease in mean horn size in bighorn sheep (*Ovis canadensis*) (Coltman *et al.*, 2003; Pigeon *et al.*, 2016), Stone's sheep (*Ovis dalli stonei*) (Douhard *et al.*, 2016), Iberian ibex (*Capra pyrenaica*), Barbary sheep (*Ammotragus lervia*) (Pérez *et al.*, 2011) and European mouflon (*Ovis gmelini musimon*) (Garel *et al.*, 2007). In fish, harvest is thought to have caused a decrease in mean body circumference in sockeye salmon (Hamon *et al.*, 2000), lower mean body mass and shorter mean body size in various salmon species (Ricker, 1981) and Atlantic cod (*Gadus morhua*) (Law & Rowell, 1993), as well as a decline in mean body size and mean age at breeding maturity in a variety of species (Law, 2000; Kuparinen & Merilä, 2007). Because body size is related to fecundity in many fish species (Wootton, 2012), a reduction in body size may affect population breeding capacity (Kuparinen & Merilä, 2007). The most famous example is provided by the Atlantic cod, where a decline in mean age and size at maturity preceded a collapse of fish stocks (Olsen *et al.*, 2004). A study on rod-fishing of large-mouth bass (*Micropterus salmoides*) showed that the fish most vulnerable to being caught were also those with the best body condition and providing the best parental care (Cooke *et al.*, 2007). Hence, in this species, the removal of only a few individuals through fishing may significantly alter the

population trajectory. Selective harvest, targeting (deliberately or not) a given morphological or behavioural character, can therefore influence a variety of life-history traits (see also pace-of-life syndromes in Dammhahn, 2018).

Besides the possible targeting of some phenotypes by fishermen and hunters, the harvest rate itself may also cause phenotypic change. Generally speaking, a strong increase in mortality (e.g. a heavy non-selective hunting pressure) will favour 'fast' life-history traits (Law, 2000; Servanty *et al.*, 2011; Kuparinen & Festa-Bianchet, 2017). Several studies on wild boar (*Sus scrofa*) support this hypothesis, showing that heavy hunting pressure leads to advanced parturition, so that females can initiate reproduction during their first year of life (Servanty *et al.*, 2009; Gamelon *et al.*, 2011). Other studies report changes in ungulate behaviour during hunting periods, with differential habitat use or migration departure being triggered by hunting in elk, red deer (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*), for example (Ciuti *et al.*, 2012; Lone *et al.*, 2015; Little *et al.*, 2016; Rivrud *et al.*, 2016).

(2) Is there evidence of phenotypic changes in birds?

Comparatively few studies have documented selection of traits through hunting in birds, and these concern only a few bird families (Table 2). For snow goose, Morez, Gauthier & Reed (2000) suggested there was preferential harvest of individuals in poor body condition among young birds. Christensen (2001) found that young common eider in poorer body condition were more vulnerable to hunting, a pattern confirmed by Guillemain *et al.* (2007) in common teal (*Anas crecca*). In North America, several studies showed that hunted mallard were in poorer body condition or of lower body mass than individuals collected by other means (Greenwood, Clark & Weatherhead, 1986; Hepp *et al.*, 1986; Reinecke & Shaiffer, 1988; Dufour, Ankney & Weatherhead, 1993; Heitmeyer, Fredrickson & Humburg, 1993; Szymanski, Johnson & Grovijahn, 2013). Although individual body condition can change rapidly in birds (Tamisier *et al.*, 1995; Robb, Tori & Kroll, 2001), it can be consistent from one year to the next (Guillemain *et al.*, 2013), and may be partly heritable (Merilä, Kruuk & Sheldon, 2001). Selectively removing individuals in poorer body condition from the population, even non-intentionally, could therefore lead to phenotypic changes, improving average fitness of the remaining individuals in the population. Grzegorzczuk *et al.* (2022) found no differences in wing length, body mass or body condition at ringing between birds harvested later and those that were not for a range of hunted bird species, hence providing no evidence for an obvious selection process by the hunters. One study showed that hand-reared ring-necked pheasants assessed as a 'bolder' behavioural phenotype were the most vulnerable upon release (Madden & Whiteside, 2014). Despite the strong potential of hunting to act as a selection pressure on birds, this topic has largely been overlooked, with most studies focussing on the direct demographic consequences for population size (see Section II), or indirect effects such as disturbance and its consequences on

Table 2. Examples of hunting selectivity in birds.

Species	Category selected by hunters	Intentionality	Reference
Mallard (<i>Anas platyrhynchos</i>)	Ducks with low body mass	Non-intentional	Greenwood <i>et al.</i> (1986); Heitmeyer <i>et al.</i> (1993)
	Ducks in poor condition	Non-intentional	Hepp <i>et al.</i> (1986); Reinecke & Shaiffer (1988); Dufour <i>et al.</i> (1993)
Common teal (<i>Anas crecca</i>)	Ducks with low body mass	Non-intentional	Guillemain <i>et al.</i> (2007)
Common eider (<i>Somateria mollissima</i>)	Individuals in poor body condition among young birds	Non-intentional	Christensen (2001)
Pink-footed goose (<i>Anser brachyrhynchus</i>)	Juveniles and adult breeders	Non-intentional	Madsen (2009)
Greater snow goose (<i>Anser caerulescens atlantica</i>)	Juvenile males and females in some years	Non-intentional	Morez <i>et al.</i> (2000)
Pheasant (<i>Phasianus colchicus</i>)	Assessed as fast and bold when they were juveniles (in males only)	Non-intentional	Madden & Whiteside (2014)
Eurasian woodcock (<i>Scolopax rusticola</i>)	Juveniles and females	Non-intentional	Christensen <i>et al.</i> (2017)
Pheasant, western capercaillie (<i>Tetrao urogallus</i>), common eider (<i>Somateria mollissima</i>)	Males	Intentional (imposed in hunting legislation)	Roth & Merz (1997); Thiel <i>et al.</i> (2007); Tjørnløv <i>et al.</i> (2019)

behaviour and distribution (e.g. Madsen & Fox, 1995). Béchet *et al.* (2003), for example, demonstrated a change in migration route by snow geese in response to spring hunting, while several studies show that the start of the hunting season can cause changes in habitat use or even trigger migration departure (Väänänen, 2001; Casas *et al.*, 2009; Palumbo *et al.*, 2019). Whether deliberate or not, with potential effects on sex and age ratios or more subtle behavioural ones (e.g. changes in habitat use), it is clear that selective effects of hunting in birds could have far-reaching consequences, and deserve greater research attention. This may not be an easy task, since most populations have been harvested for an extended period of time, so that current populations may already have been affected by an extended harvest selection process.

(3) Selection does not equate to evolution

Selective harvest can have evolutionary consequences on wildlife populations only when certain conditions are met (Festa-Bianchet, 2017). First, the trait under harvest selection has to be heritable. In fish, body size, length and age at maturity are to a large extent heritable (Law, 2000). In mammals, 20–40% of variability in horn and antler size is heritable (reviewed by Festa-Bianchet & Mysterud, 2018). In birds, some morphological and behavioural traits possibly under hunting selection (however, see Grzegorzczak *et al.*, 2022) also show some heritability: wing length (Lessells & Ovenden, 1989), tarsus length (Smith & Zach, 1979), and migration departure date (Pulido *et al.*, 2001).

In order to counter or magnify the effects of natural or sexual selection, artificial selection through harvest must exert a significant pressure on the targeted phenotypes. A wide range of parameters will affect the strength of artificial selection. In fish, for example, two main parameters seem to act in concert on the strength of the selection induced by harvest: (i) harvest

volume or the proportional share of the overall mortality caused by fishing; and (ii) the relative size of harvested individuals (Stokes & Law, 2000; Kuparinen & Merilä, 2007). In some fish stocks, the selection pressure caused by harvest is extremely high, since fishing mortality is 3–5 times greater than natural mortality (Stokes & Law, 2000).

In mammals, hunting often targets secondary sexual characters such as horn or antler size, which are also subject to sexual selection in the opposite direction. Thus, in order to alter the evolutionary trajectories of populations, selection by hunting must be strong enough to counter the effects of sexual selection (Festa-Bianchet & Mysterud, 2018). It can be difficult to determine the exact role of secondary sexual characters on breeding success, but in species where horns and antlers grow fast and are used as stabbing weapons, such as roe deer (*Capreolus capreolus*), mountain goat (*Oreamnos americanus*) or chamois (*Rupicapra rupicapra*), their size appears to play a lesser role in mating and breeding success (Festa-Bianchet, 2012). Conversely, in species in which these secondary traits grow slowly and are used to push the opponent (e.g. European mouflon, Iberian ibex, red deer), horn and antler sizes play a greater role in access to reproduction and breeding success. The evolutionary impact of trophy hunting is therefore likely to be greater in the latter cases, where removing an older individual with large horns/antlers will have a greater effect on access to reproduction among the surviving individuals (Festa-Bianchet & Mysterud, 2018). Finally, social organisation may affect the evolutionary consequences of hunting. For example, in gregarious species it is easier for a hunter to assess relative size and hence target bigger individuals and/or those with the largest horns/antlers (Festa-Bianchet, 2017), potentially making harvesting a greater selection pressure than in solitary species. In species which form family groups for one or more years, the naïve behaviour of young individuals (e.g. Clausen

et al., 2016) may lure their parents within shotgun range, so that selective hunting may occur towards the most productive adult individuals (D. Koons, personal communication).

Artificial selection through harvest has to be strong, persistent, and has to occur over large areas and over many generations to have a significant evolutionary impact (Festa-Bianchet & Mysterud, 2018). Selection through harvest is likely to be stronger when individuals are harvested before their first breeding attempt (Coltman *et al.*, 2002), or when individuals with the greatest breeding contribution to the dynamics of the population are targeted (that is, before senescence; Williams, 2001). Selection also has a greater evolutionary impact when both sexes are harvested for the same criteria (Festa-Bianchet, 2017). Conversely, the impact of selection through harvest may be buffered or entirely cancelled when individuals from hunting-free areas can migrate into the area of exploitation (Tenhumberg *et al.*, 2004), or when polygenic traits under genetic covariation are selected (Morrissey *et al.*, 2012). A recent study did not find strong evidence for selective hunting on morphological traits in a range of bird species (Grzegorzcyk *et al.*, 2022). However, since these species have long been hunted, selection might have already occurred and no longer be detectable. Assessing whether other selection mechanisms occur during harvest is a clear perspective for future research in this taxonomic group, and will be necessary for assessment of the potential evolutionary consequences of harvest.

(4) Plasticity or evolution?

Even if conditions are often met that make harvest a likely evolutionary force, it remains difficult to assess whether observed phenotypic changes reflect selection in a population or result from phenotypic plasticity (Kuparinen & Festa-Bianchet, 2017; Heffelfinger, 2018; Kardos, Luikart & Allendorf, 2018). Indeed, phenotypic changes caused by the environment or by relaxation of density-dependent processes may have similar results to those caused by selective exploitation. In ungulates of temperate areas, for example, reduced population density caused by hunting during the autumn releases interspecific competition during winter, allowing advanced breeding (Kuparinen & Festa-Bianchet, 2017). Thus, mechanisms such as density dependence or the action of confounding factors could magnify the effects of selective hunting or give the illusion that selective hunting is taking place (Kuparinen & Festa-Bianchet, 2017). For example, trophy hunting has long been considered the potential cause of an evolutionary decrease in mean body mass and horn size in some ungulates (e.g. Festa-Bianchet, 2007), but some studies have shown that such changes occur in response to climate warming (for example in chamois; Rugheiti & Festa-Bianchet, 2012). Similarly, an increased water temperature is expected to cause reductions in mean body length in fish (Daufresne, Lengfellner & Sommer, 2009; Sheridan & Bickford, 2011; Cheung *et al.*, 2013); the same reduction expected from selective harvest of larger

individuals. Therefore, environmental changes such as climate warming can complicate isolation of the effects of selective harvest.

It is also often difficult to identify the potential genetic basis of the observed changes. In order to differentiate selection from a plastic individual response, one should ideally identify the gene(s) responsible for the focal phenotypic variability and link phenotypic changes to changes in gene frequency (Festa-Bianchet & Mysterud, 2018). However, such data are rarely available for exploited wildlife populations. When genetic data are not available, tracking changes in reaction norms measured at the population level could be a powerful tool to determine whether observed phenotypic changes result from genetic evolution or plasticity (Heino & Dieckmann, 2008). Reaction norms can be defined as the range of phenotypes expressed by a given genotype exposed to various environmental conditions (Schmalhausen, 1949). Because it is not always possible to test a single genotype against all possible environmental conditions, one can track phenotypic changes at the population level and assess whether the observed changes result from changes in reaction norm (and thus the genetic structure of the population) or from the phenotypic expression of individuals. Changes in genetic structure (e.g. triggered by non-random harvesting of certain phenotypes) are expected to cause both a shift and a reduction in width of the distribution range of phenotypic expression (a proxy for reaction norm), whereas plastic responses would cause a phenotypic range shift only (Ernande, Dieckmann & Heino, 2004). In species where reaction norms are not characterised, such as ungulates, it is possible to use changes in policy and associated changes in hunting selection pressure over time to monitor possible changes in phenotype such as horn/antler size (Pigeon *et al.*, 2016).

As stated above, selection pressure induced by human exploitation can be very high. For instance, Darimont *et al.* (2015) showed that human-induced mortality is far greater than any other source of predation: fisheries have a median exploitation rate up to 14 times greater than marine predators. In this context, phenotypic changes induced by exploitation are potentially much faster and larger than those that take place in response to other anthropic and natural factors (Darimont *et al.*, 2009). It remains unsettled in the scientific community if it is necessary to establish clearly the mechanism underlying phenotypic changes caused by harvest (Allendorf *et al.*, 2008). On the one hand, the population response may vary depending on whether a genetic response or plasticity is involved. When observed phenotypic changes mostly result from a genetic response (i.e. changes in the frequencies of genotypes), returning to the initial phenotypic structure after alleviation or cessation of harvest will be more difficult, as this would require a backwards evolutionary process (Hutchings & Fraser, 2008). This is called a 'Darwinian debt' (e.g. Pandolfi, 2009), and is an important notion in harvest management based on the idea that natural selection is sometimes weaker than artificial selection.

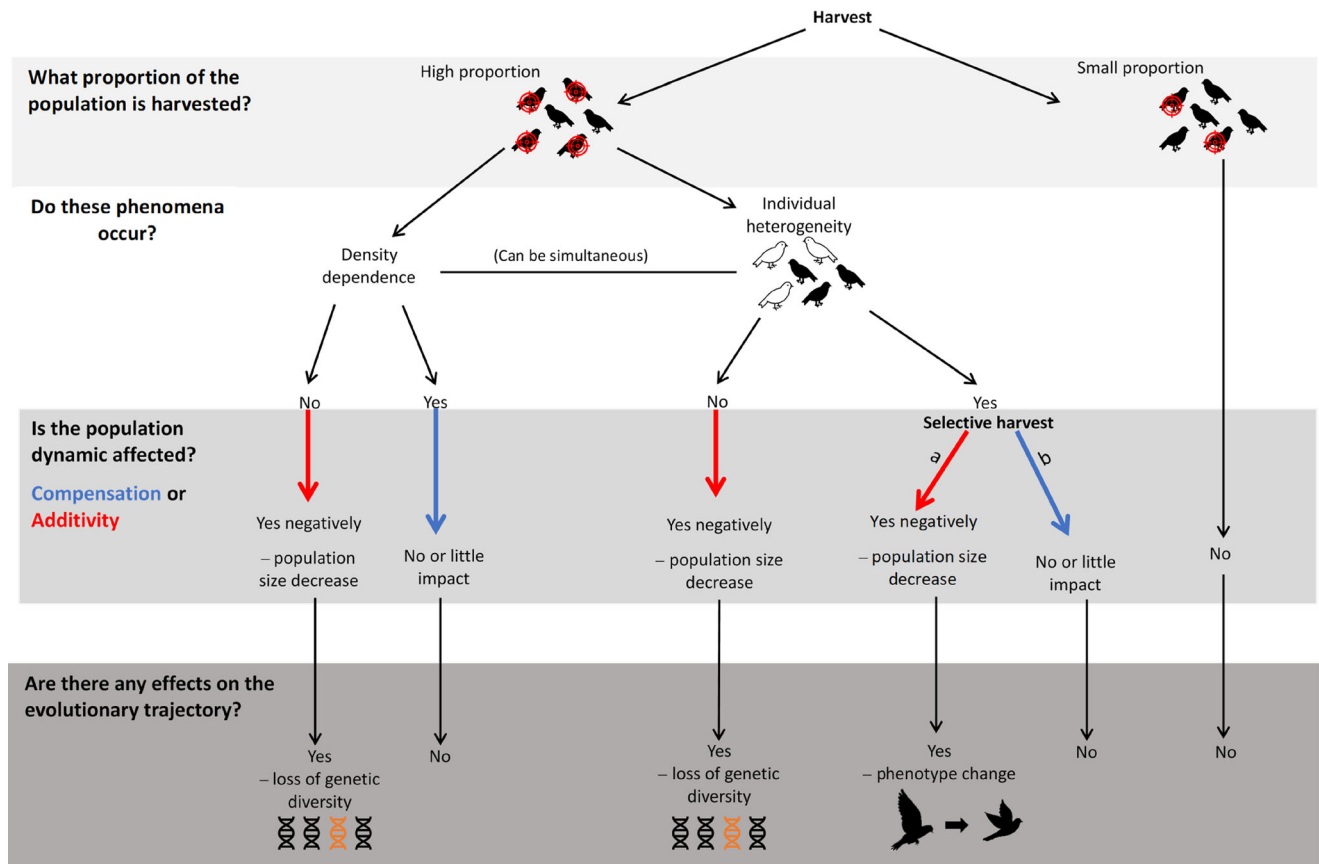


Fig. 2. Demographic and evolutionary responses of a wild bird population to harvesting. Blue arrows illustrate cases where part of the mortality induced by harvest is fully or partially compensated by the population, owing either to density-dependent processes or heterogeneity among individuals. Red arrows illustrate cases where harvest-induced mortality is instead additive to other sources of mortality, either because density-dependent processes do not occur or there is no heterogeneity in the population. The letter ‘a’ illustrates a case where the selective harvest is carried out on individuals that contribute the most to the growth rate of the population (better survival and/or reproductive capacity); the letter ‘b’ indicates the opposite case where individuals that contribute the least to the growth rate of the population are preferentially harvested.

The Darwinian debt predicts that if exploitation alters genotype frequency and variability, a much longer time may be necessary for populations to recover the initial optimal phenotypic landscape, altering their capacity to cope with environmental changes (Allendorf *et al.*, 2008). Assessing whether observed phenotype changes result from phenotypic plasticity or changes in gene frequencies is therefore critical to determining the ability of a population to return to the initial pre-exploitation state following selective harvest. Even when observed changes result from phenotypic plasticity, they may have undesirable consequences on individual fitness and hence population dynamics until harvest pressure is relieved.

This review of the possible impacts and evolutionary consequences of harvest on wildlife populations shows that, to date, most research has concerned mammals (especially ungulates) and fish, probably due to their economic importance and because of the relative ease with which phenotypic changes can be studied in these taxa (e.g. body size, antler and horn size). The massive harvest of wild birds at a worldwide scale

likely also causes phenotypic changes that may have a genetic basis, yet this has not been a focus of research. We can build on the strong theoretical framework provided by existing studies on fish and mammals, creating a stimulating avenue for future research in birds with implications for the future management and conservation of their populations. Figure 2 summarises the possible pathways by which harvest can eventually have evolutionary consequences in birds.

IV. CONCLUSIONS

- (1) Hunting is a very popular activity, either as a leisure activity or for subsistence in various parts of the world. The annual hunting bag for birds amounts to tens of millions of individuals in many geographic areas, and some birds are textbook examples of how overexploitation can lead to species disappearance.
- (2) Birds have long been important models for analytical demographic research and many of the studies and debates

about the compensatory–additivity process were based on bird studies, especially waterfowl. Birds are also popular among the public, hunters, bird watchers, and scientists. They are hence a focus of attention and their study produces huge amounts of data annually *via* population censuses and ringing schemes.

(3) This literature review highlights some major recent advances in demography, such as the ability to evaluate and consider hidden individual heterogeneity in population dynamics models. Such technical advances plus the huge quantity of data available provide unequalled opportunities for future research, for the better management and conservation of bird populations and to promote demographic knowledge more generally, beyond birds.

(4) The possible impact of harvest on phenotypic traits has received much attention in mammals and fish, highlighting conditions under which hunting and fishing may have evolutionary consequences. The massive annual hunting bags and hunting pressure exerted on bird populations suggest that harvest should also be an important evolutionary force in this taxonomic group. However, beyond sex and sometimes age classes, most individuals from a given species look alike in birds, so that the potential for conscious selective hunting can seem unlikely and has therefore almost entirely been overlooked in birds.

(5) Knowledge gained from mammals and fish regarding the evolutionary impacts of harvest provide a favourable scientific context for similar research in birds. However, the extent to which bird hunters are selective towards some traits, whether deliberate or not, deserves further research. In particular, whether selection and evolution can occur on behavioural and personality traits has not been tested and would deserve future investigation.

(6) Biological samples (blood, flesh, or other tissues) can easily be obtained from harvested animals. These could be used with modern genomic analyses to compare the effects of differential hunting pressures on genetic signatures among different populations or flyways of the same bird species, or to trace past changes in such harvest rates over a species history through remaining genetic variability. Such studies will enable a better understanding of the links between past and present hunting and evolution in birds, with the aim of improving hunting management and ensuring sustainable populations in the future for this charismatic taxonomic group.

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