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Current management

Hunting of migratory birds: disturbance intolerant or harvest tolerant?

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An understanding of how hunting affects migratory birds is essential for reaching sustainable management of hunted populations. The purpose of our paper was to synthesise current knowledge of autumn and winter hunting disturbance on migratory birds and to describe a case study in Hellas (Greece). Hunting may influence migratory bird behaviour and movements, but studies have not found a corresponding increase in non-hunting mortality factors or any reduction in feeding, body condition, breeding success and any long-term population decrease. We developed a diagnostic procedure which provides a tool for assessing the potential susceptibility of a species or group of species to hunting disturbance. The application of this procedure showed that the influence of hunting disturbance on quarry species is inverse to hunting harvest. This new insight should be considered in a holistic hunting management approach.

Key words: birds, energetics, EU Directives, habitats, hunting regulations, sustainability, trade off

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Numerous studies have documented the effects of hunting disturbance on birds (Madsen & Fox 1995, Gill et al. 2001, Tamisier et al. 2003, Dooley et al. 2010). Despite this research, there is little information about the relative importance of disturbance to populations compared to harvest impact to populations (Harradine 1998, Gill et al. 2001). Often disturbance resulting from hunting is not included in discussions about sustainable harvest management (Aebischer 1997, Sutherland 2001, Elmberg et al. 2006, Nichols et al. 2007). Nevertheless, extensive spatio-temporal restrictions on hunting have been proposed due to disturbance (e.g. Tamisier 2005, Casas et al. 2009) although such restrictions may not increase populations at a regional or flyway level (Brochet et al. 2009).

A common problem in conservation science and policy is the failure to distinguish critically important conservation issues from trivial issues (Caughley 1994, Sutherland 2000). Too often disturbance caused by hunting is presumed to be harmful without substantiation (Harradine 1998). Consequently, the responsible agencies evoke hunting disturbance as reason for additional hunting restrictions (Harradine 1998, European Commission 2001) even though other factors may cause the similar disturbance, e.g. walking (Dooley et al. 2010) or greater disturbance such as aircraft and intentional scaring by farmers (Norriss & Wilson 1988, Klaassen et al. 2006).

Hunting restrictions are often supported by hunters (Lee & Chun 1999), and they have demanded the establishment of many refuges (Schou & Bregnballe 2007). Hunting management is necessary because excessive hunting activity may lead to poor harvest success, over-crowding and unsatisfactory experiences for hunters (Madsen et al. 1998, Lee & Chun

1999). Hunting was increased in wetlands around a new hunting closure in Camargue, southern France (Mathevet & Tamisier 2002). However, Madsen (1998b) noted that after the establishment of refuge areas in two Danish wetlands, the number of hunters declined into one hunting area of the first wetland, and the number of hunters did not decline but were redistributed in the other wetland.

Few attempts have been made to synthesise available knowledge of hunting disturbance and harvest management. The aims of this review were to: 1) explore the somewhat circular discussion of the current literature on hunting disturbance, especially on waterfowl, 2) suggest an analytical diagnostic procedure for evaluating tolerance of migratory hunted bird species to disturbance, 3) apply this procedure in a case study in Hellas, and 4) compare disturbance tolerance with harvest tolerance and provide guidance on hunting management.

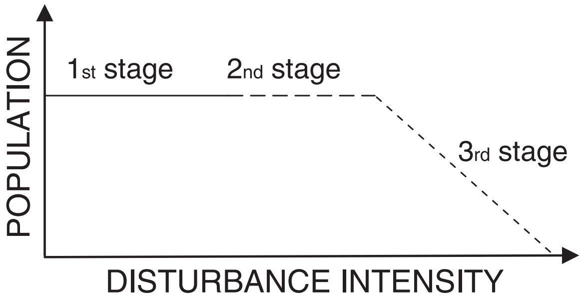

Figure 1. Stages of hunting-disturbance influence on population. During phase 1 there are only effects, during 2 there are impacts, which do not cause population decrease because of compensatory mechanisms, and during 3 there are additive impacts causing population decrease.

Effects vs impacts of hunting disturbance

We define effects as observable responses by bird species, usually short-term, in numbers, distribution or behaviour on given sites (for example, a temporary displacement of birds away from a site; Fig. 1). Impacts imply a reduction in survival of individuals, which may cause declines in population size (Hill et al. 1997, Gill et al. 1998). Nevertheless, Blanc et al. (2006) suggested that these two interdependent notions are associated with two distinct organisation levels: 'effects' on individuals and 'impacts' on populations.

Assessing the severity of disturbance has important practical consequences; if disturbance has serious impacts, then conservationists are justified in recommending more restrictive management measures such as limiting access to wildlife areas (Tuite et al. 1984, Klein et al. 1995). However, if impacts of disturbance are trivial and there is no site specific and documented necessity, then such measures cannot be justified. Excessive restrictions on human access to wildlife areas can have socio-economic costs, but, more importantly, the restrictions are contrary to the view that access to countryside should be increased (Gill 2007). Properly controlled access to countryside can be the best way to protect nature, as it enhances its importance for society (King & Lester 1995, Adams 1997, Harradine 1998, Gill 2007).

So, what constitutes a serious impact due to hunting disturbance on migratory bird quarry species? Article 2 of the European Union Birds Directive (2009/147/EU) contains the general obligation on Member States to "take the requisite measures to maintain the population of the species referred to in Article 1 at a level which corresponds in particular to ecological, scientific and cultural requirements, while taking account of economic and recreational requirements, or to adapt the population of these species to that level". Thus, the conservation impact for a quarry species is serious only when there is a population decrease that has consequences for conservation status of this or another species, hunting sustainability and quality. This could be defined as a long-term population impact. To examine this, the possible hunting disturbance consequences for bird quarry populations and the scientific findings should be investigated (Fig. 2).

Non-hunting mortality factors

Few data are available that document the influence of hunting disturbance on other mortality factors. Thrushes of the *Turdus* genera are important quarry species, with annual bags comprising many tens of millions of birds (Aebischer et al. 1999). Payevsky & Vysotsky (2003) used ringing recoveries of song thrushes *Turdus philomelos* and compared survival rates between a hunted and a non-hunted population. They found that in the British Isles, where the song thrush is mainly a resident and not hunted species, adult survival rates did not differ from the rates obtained for the Baltic migrating and hunted population, whereas first-year survival was somewhat higher for the British Isles population than the Baltic. Baltic thrushes had nearly the same mortality

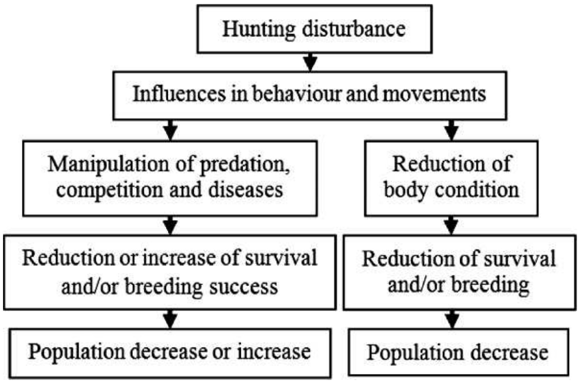

Figure 2. Possible influences of autumn and winter hunting disturbance. Hunting disturbance could manipulate predation and competition, if the predators and competitors are themselves sensitive to hunter's activities. Moreover, pathogen transmission may be modified due to changes in movement and density of birds.

as thrushes from the British Isles although they are harvested and disturbed, indicating the relatively low or compensated impact of hunting (Payevsky & Vysotsky 2003).

In a study of woodcock *Scolopax rusticola*, Duriez et al. (2005) found that there was similar predation rates (by natural predators) between non-hunted and hunted areas of France. McAuley et al. (2005) studied survival of American woodcock *Scolopax minor* during the hunting season. They used radio-telemetry to determine survival rates and causes of mortality for 913 woodcock captured during fall 1997-2000 in seven areas, three of which were closed to hunting. They found that two of the hunted areas had the highest daily survival rates for non-hunting factors, while two other hunted areas had rates similar to the three non-hunted areas. The authors suggested that hunting is not the cause of the population decline, and indicated that harvest under the current regulations did not result in lower survival rates of woodcock.

In some cases, hunted bird species survival is decreased by severe cold weather (e.g. woodcock; Tavecchia et al. 2002), but there are species for which this fact does not hold (e.g. mallard *Anas platyrhynchos*; Boos et al. 2007). During severe weather periods, hunting disturbance may aggravate the consequences from non-hunting factors. However, in this case statutory hunting suspension was applied in many European countries (e.g. Stroud et al. 2006, personal communication with managers from several European countries).

Feeding and body condition

Disturbance is thought to most likely have an impact on bird populations during periods of food scarcity or when birds have difficulty meeting their energy and nutrient requirements (Madsen 1995). Gaston (1991) studied the effect of hunting on body condition of gadwalls *Anas strepera*. His results showed that lipid reserves increased when hunting was suspended, but he also concluded that such simple relationships alone are inadequate tests and that other factors like temperature also have an influence.

Theoretically, local displacements and reduced stop-over times may have long-term impacts on populations. Evans & Day (2001) reported changes in diving duck movements, but concluded that any energetic consequence is likely to be small. Jamieson et al. (2006) found that there were no significant relationships between lipid levels and hunting disturbance of northern common eiders *Somateria mollissima borealis* wintering in southwest Greenland. Similarly, Casas et al. (2009) found that hunting activity increased flight probability and time spent vigilant, but did not affect the time spent feeding. Moreover, hunting might actually conserve food resources for spring feeding by causing redistribution (NERI 1996).

Under certain conditions, birds can show physiological and behavioural adaptability. In particular, many goose species adapt to hunting disturbance by increasing their nocturnal feeding activity (Raveling et al. 1972, Giroux & Bédard 1988, Riddington et al. 1996). Belanger & Bedard (1990) reported that disturbed greater snow geese *Chen caerulescens atlantica* spent 52 seconds per flight and lost 4-51% of their diurnal feeding time; however, the increase in nighttime feeding and daily feeding rate were compensatory mechanisms to energetic cost caused by hunting disturbance. Nevertheless, > 2 disturbances per hour may cause an energy deficit that no behavioural compensatory mechanism can counterbalance (Belanger & Bedard 1990).

Special spring hunting seasons in USA had negative effects on behaviour of staging greater snow geese, and may ultimately adversely affect their body condition (Mainguy et al. 2002, Féret et al. 2003, Bechet et al. 2004). This special hunting period (15 April - 31 May) was held when intense fat and protein accumulation took place and just prior to the reproduction period (middle of June). Therefore, results from these studies should not be interpreted as also applying to autumn and winter hunting, because in the early stages of migration fattening is not as important for geese as in later stages (Madsen 2001b, Bauer et al. 2006).

Refuge theory and foraging resource depletion have been used to explain movements and use of foraging habitats by waterfowl during winter (e.g. Frederick et al. 1987, Vickery et al. 1995, Borbach-Jaene & Kruckenberg 2002). Daily movement distances are probably proportional to energy expenditure and potential exposure to mortality (Frederick et al. 1987). Assuming these movements are adaptive, costs and risks associated with increased movements are predicted to be outweighed by potential fitness benefits to individuals (Hamilton & Watt 1970). Frederick et al. (1987) found that when abundant food was provided on the refuge, hunting mortality was reduced and waterfowl use of the refuge increased. Thus, when food resources are more plentiful the influence of disturbance is reduced (Madsen 1995).

Particularly in the lowlands of the Mediterranean, where many migratory quarry species winter in Europe (McCulloch et al. 1992, Hagemeijer & Blair 1997), the availability and nutritional quality of food are likely not limited for some species. In contrast to Central and North Europe, in the Mediterranean Basin days are longer and the nutrients of forage plant species are of maximum value at the end of the winter and the beginning of spring (e.g. Papanastasis 1982, Prop & Deerenberg 1991). Fruits of many woody plants are mature (e.g. olives) and provide nutritious food for the birds (Bairlein 1987, Sokos et al. 2009). Arzel et al. (2009) found that the Mediterranean wetland of Camargue offered teal *Anas crecca* more seed food than any studied site of northern Europe. Also, the weather is milder in the Mediterranean than in Central and North Europe and this means shorter foraging periods when moving northwards (Guillemain et al. 2002).

Moreover, there is a cost incurred by carrying fat in terms of an increasing mass-dependent predation risk through a decline in maneuverability and flight performance on take-off (Lima 1986, Witter & Cuthill 1993, Metcalfe & Ure 1995, Cresswell 1998). For this reason birds should carry the minimum fat reserves needed (Gosler 1996, Cresswell 1998).

Breeding success

The only study we could find that relates hunting to reproduction is the study of Bety et al. (2003). They tracked radio-marked female greater snow geese at their main spring staging area and on their breeding grounds and found that spring hunting at staging areas did not influence breeding success.

The hunting season in Europe ends at least one or two months before the reproduction period (Cramp et al. 1977-1994). Thus, questions of whether there is any influence of disturbance on breeding success are raised. Species which depend on endogenous sources for breeding (capital breeders) may be more sensitive to hunting disturbance than species which depend on exogenous sources (income breeders), because the latter could replenish the energy and nutrients soon after the hunting period.

Madsen (1995) reports that the pink-footed goose *Anser brachyrhynchus*, a capital breeder, is capable of building reserves that were consumed during the flight from Denmark to northern Norway within one to three weeks. This time interval seems to be adequate so geese can start incubation without energetic deficiencies (Arzel et al. 2006). MacCluskie & Sedinger (2000) concluded that endogenous nutrient availability does not proximately limit clutch size during laying for shovelers *Anas clypeata*, possibly due to the high productivity of wetlands in breeding areas that allow females to forage extensively. Late winter body condition of teal, an income breeder, was positively correlated with the proportion of juveniles in the population the following autumn (Guillemain et al. 2008); however, the proportion of juveniles in the population was not correlated with breeding success in Finland (Guillemain et al. 2010). For other bird species, results from the analysis of stable isotopes indicate that endogenous nutrients do not play a role in egg formation of several shorebird species in the Arctic (Klaassen et al. 2001).

Population effects

Studies have reported changes in behaviour and movements of migratory quarry species due to hunting (e.g. Madsen & Fox 1995, Casas et al. 2009). Several other studies demonstrated that ducks returned to disturbed areas after disturbance ended (Parrish & Hunter 1969, Dooley et al. 2010). This was confirmed by observations in areas of botulism infection, where shots were deliberately fired to drive ducks away to prevent infection. This proved, however, to be impossible as the ducks returned to the preferred area shortly afterwards (Parrish &

Hunter 1969). Dooley et al. (2010) found that a high proportion of mallards exposed to walking and shooting disturbance returned to treatment locations in $\leq$ 1 day.

At the flyway level, Maisonneuve & Bedard (1992) neck-banded 2,150 greater snow geese to study autumn stop-over from 1985 through 1987. Birds using primary sites where hunting pressure was higher did not have shorter stop-over duration than others. For the same species and region, Bechet et al. (2003) found that radio-tagged geese made more backward movements along a 600-km route after the beginning of the special spring hunting. In Scotland, Percival et al. (1997) found that although disturbance slightly increased the emigration rate of wintering marked barnacle geese *Branta leucopsis*, many individuals persisted in using heavily disturbed sites. Moreover, there were some indications from bird counts that during fall migration waterfowl stayed longer in northern areas when refuges were created (Madsen 1998b) or hunting period was shortened (Moore & Black 2006). No indication was given that these behavioural responses to autumn and winter hunting affected the populations.

A species with suitable habitat nearby may avoid disturbance simply because it has alternative sites to use (Gill et al. 2001). For example, wigeon *Anas penelope* move readily in response to disturbance (Madsen 1998b), but may be able to do so because habitat in the area is abundant. This is important for management because, although it seems that species that move easily when disturbed are those that are in need of most protection, in fact, these may be the species for which the cost of moving is smallest, and hence they are not in need of protection (Gill et al. 2001). Beale & Monaghan (2004) tested the link between individual state and responsiveness to disturbance by manipulating condition by providing supplementary food for turnstones *Arenaria interpres*. Birds, whose condition had been enhanced, showed higher responsiveness to certain human disturbance, flying away at longer distances from the observer, scanning more frequently for predators and flying further when flushed.

Brochet et al. (2009) reported that the increase of the total hunting closure area and hunting period restrictions (closing dates were staggered from the beginning of February according to species, taking differences in spring migration phenology into account) did not result in an increased population of ducks in the Camargue (France).

A diagnostic procedure for assessing disturbance and harvest: Hellas as case study

Hunted bird species have different species-specific traits and habitat and can be subject to different management and hunting methods and pressure. These factors are important when considering a species' tolerance to disturbance from hunting (Hill et al. 1997, Madsen et al. 1998, Laursen et al. 2005). Madsen et al. (1998) suggested an index of five factors to express the tolerance of individual species to disturbance. We modified this index and developed a diagnostic procedure with nine factors for assessing harvest-related disturbance. These factors include:

1) Nocturnal feeding ability: a species with the ability to feed at night is less susceptible to hunting disturbance (Belanger & Bedard 1990, Riddington et al. 1996, Dooley et al. 2010);
2) Family group, flock size: hunting disturbance may be greater for quarry species occurring in groups or flocks because it may disrupt the group integrity (Bartelt 1987). Moreover, flight distances are increased with flock size (Madsen et al. 1998, Laursen et al. 2005);
3) Response to disturbance: seeking nearby cover after being disturbed (Baaziz & Samraoui 2008, Cresswell 1998) should increase a species tolerance to hunting disturbance compared to species that make long flights or, more rarely, leave the area following disturbance (Frederick et al. 1987, Dooley et al. 2010);
4) Food availability, quality and requirement: plentiful and nutritious food resources reduce the influence of hunting disturbance (Madsen 1995);
5) Habitat availability: species with restricted habitat are more intolerant of hunting disturbance because they may make more flights, move to unsuitable habitat or move to another region (Frederick et al. 1987, Madsen et al. 1998, Dooley et al. 2010);
6) Predator disturbance: dabbling ducks are disturbed up to 130-160 times/day by avian predators (Tamisier 1974, Fritz et al. 2000). Predators' disturbance is different between species; for example, teal make more flights than mallard due to raptors (Johnson & Rohwer 1996);
7) Refuges: species with a higher percentage of their habitat within hunting closure areas or areas not accessible to hunters (e.g. sea) are more tolerant to disturbance (Madsen et al. 1998);

8) Hunting method: species subject to mobile hunting activity close to roosting and/or feeding areas are more susceptible to hunting disturbance than species subject to harvest from fixed points or species that are hunted as they move between areas (Fox & Madsen 1997, Evans & Day 2001);
9) Hunting status: popular quarry species which are hunted frequently and where hunter density is high are more intolerant of hunting disturbance (Madsen et al. 1998).

We used four hunting managers (including the two first-mentioned authors) and one experienced hunter to independently evaluate the parameters of our diagnostic procedure (Table 1) in Hellas.

In the case of harvest (see Table 1), Harvest tolerance (Harv) can be estimated as the sum of Hunting status (Hs) and Hunting success (Suc). Suc is defined as the quarry species harvested per quarry species found or seen by a hunter during its daily excursion (Thomaides et al. 2011). Suc is dependent

Table 1. Diagnostic procedure of quarry migratory bird species' tolerance to hunting disturbance shown as the sum of nine factors and harvest shown as the sum of two factors. Information on food, habitat and behaviour was obtained from descriptions extracted from Cramp & Simmons (1977-1994), Madsen et al. (1998) and Kazantzidis et al. (2007). For the factors Night and Pred, information was obtained from [1]Campbell & Tobler (1984), [2]Jiang et al. (2007), [3]Thomas et al. (2006), [4]Eraud & Corda (2004) and [5]Johnson & Rohwer (1996). Information on success and hunting status was found in Kazantzidis et al. (2007) and Thomaides et al. (2011).

	Factors										Factor	
Quarry species	Night	Flock	Resp	Food	Hab	Pred	Ref	Hm	Hs	Dist	Suc	Harv
Anser albifrons	1[1]	-1	-1	-1	-1	1	1	0	-1	-2	2	1
Anas platyrhyncos	1[1.2]	0	-1	0	-1	0[5]	1	1	-1	0	2	1
Anas strepera	1[1.2]	0	-1	-1	-1	0	1	1	-1	-1	2	1
Anas crecca	1[1.2]	0	0	0	0	-1[5]	1	1	-1	1	2	1
Anas acuta	1[1.2]	0	-1	0	-1	0	1	1	-1	0	2	1
Anas clypeata	1[1.2]	0	-1	0	-1	0	1	1	-1	0	2	1
Anas querquedula	1[1.2]	0	0	0	0	-1	1	1	0	2	2	2
Anas penelope	1[1.2]	0	-1	-1	-1	0	1	1	-1	-1	2	1
Aythya ferina	1[1.2]	0	0	0	0	0	1	1	0	3	2	2
Aythya fuligula	1[1.2]	0	0	0	0	0	1	1	0	3	2	2
Fulica atra	1[2]	-1	1	-1	0	0	1	0	0	1	2	2
Gallinula chloropus	1[2]	1	1	0	0	0	1	0	1	5	0	1
Vanellus vanellus	1[3]	-1	-1	0	0	0	1	0	0	0	2	2
Gallinago gallinago	1[3]	1	0	0	0	1	1	-1	0	3	2	2
Scolopax rusticola	1[3]	1	1	0	1	0	0	-1	-1	2	-2	-3
Columba palumbus	-1[1]	-1	-1	1	1	0	0	1	-1	-1	2	1
Streptopelia turtur	-1[1]	0	0	1	0	0	0	1	-1	0	1	0
Turdus merula	-1[1]	1	1	1	1	-1	0	0	-1	1	1	0
Turdus philomelos	-1[1]	1	1	1	1	-1	0	0	-1	1	1	0
Turdus iliacus	-1[1]	1	1	1	1	-1	0	0	0	2	2	2
Turdus viscivorus	-1[1]	0	0	1	1	0	0	0	0	1	2	2
Turdus pilaris	-1[1]	0	0	1	1	0	0	0	0	1	2	2
Coturnix coturnix	-1[1]	1	1	1	1	0	-1	-1	-1	0	-2	-3
Alauda arvensis	-1[4]	0	1	0	1	-1	-1	0	1	0	2	3
Sturnus vulgaris	-1[1]	-1	0	0	1	0	-1	0	1	-1	2	3

Night: Ability for night feeding (-1: no, +1: yes).
Flock: Family group or flock size when hunter meets the birds (-1: large; 0: intermediate; +1: small, independent individuals).
Resp: Response to hunting disturbance (-1: long flight; 0: intermediate; +1: short flight or cryptic behaviour).
Food: Food availability and quality (-1: herbivorous, 0: omnivorous, carnivorous and seed-eaters, +1: fruits from trees and oil seed-eaters with plentiful food).
Hab: Habitat availability (-1: restricted, 0: intermediate, +1: extended).
Pred: Predation pressure (-1: large; 0: intermediate; +1: small).
Ref: Refuges (-1: small percentage of available habitat, 0: intermediate, +1: high percentage of available habitat).
Hm: Hunting method (-1: search or repeated disturbance from hunter, 0: both, +1: stand hunting).
Hs: Hunting status (-1: popular quarry; 0: intermediate; +1: not popular quarry).
Dist: Disturbance tolerance is the sum of previous parameters (a higher value means higher tolerance).
Suc: Hunting success (quarries harvested per quarries found or seen by hunter during its daily excursion: -2 > 40%, -1 = 30-40%, 0 = 20-29%, +1 = 10-19%, +2 = 0-9%).
Harv: Harvest tolerance, defined as the sum of Suc and Hs (a higher value means higher tolerance).

mainly on the abundance of species and spatio-temporal hunting prohibitions. For example, as thrushes occur numerously, a hunter may harvest proportionally fewer individuals. In case of waterfowl, refuges and time restrictions during day and night do not permit hunters to approach and harvest these species. We gave a higher weight to Hunting success (five levels) than to Hunting status (three levels) because: 1) Suc is subject to lower variation between areas than Hs (e.g. hunting traditions) and 2) Suc is based on data of Hellenic National Harvest Monitoring and thus is estimated more accurately (Thomaides et al. 2011).

In Hellas there are 200.000 hunters (M.E.E.C.C. 2011), and about 80% of the total hunting excursions are focused on migratory bird quarry species (Thomaides et al. 2011). In recent years, migratory bird hunting has been restricted, with staggered closing dates during February due to Article 7.4 of 79/409EEC. Nocturnal hunting and the use of decoys and calls are prohibited. The total hunting closure area covers 9% of the Hellenic countryside (Tsachalidis 2009). However, in wetlands hunting is prohibited on about 80% of the total wetland area (Sokos et al. 2002).

All the species in Table 1 are migratory and hence harvested in a series of countries; thus for some species, we do not know the harvest status at the population level, especially for the species that visit Africa. Within Hellas our evaluation identified five categories of migratory quarry species (see Table 1):

1) species which are not popular quarries including moorhen *Gallinula chloropus*, skylark *Alauda arvensis* and starling *Sturnus vulgaris*, and thus hunting disturbance is unlikely to cause any impact on the populations;
2) species which are tolerant to disturbance and have low harvest including garganey *Anas querquedula*, common snipe *Gallinago gallinago*, coot *Fulica atra*, *Aythya* spp. and redwing *Turdus iliacus*, and thus hunting disturbance is unlikely to cause any impact on the populations;
3) species which are intolerant to disturbance, however, have low harvest including greater white-fronted goose *Anser albifrons*, wigeon *Anas penelope*, lapwing *Vanellus vanellus* and wood pigeon *Columba palumbus*, and thus hunting is unlikely to cause any impact on the populations;
4) species which suffer a high harvest, although they are tolerant to disturbance including woodcock, blackbird *Turdus merula* and song thrush, and thus hunting disturbance is unlikely to cause any impact on the populations;
5) species which have intermediate intolerance to disturbance and suffer a high harvest including quail *Coturnix coturnix* and secondly turtle dove *Streptopelia turtur*. These species have additional similarities. Both are hunted for a relatively short period at the beginning of the hunting season (end of summer until the middle of autumn) and thus harvest and disturbance occur far from the forthcoming breeding period, in contrast to all the other species. Early hunting is usually more compensatory than late hunting (Kokko 2001).

Conclusions and management implications

Our review suggests that hunting disturbance often has an effect on the behaviour and movements of birds, but this does not imply an impact on a population for species that are subject to autumn and winter hunting disturbance. Studies have not reported any non-hunting mortality increase (Payevsky & Vysotsky 2003, Duriez et al. 2005, McAuley et al. 2005), any reduction in feeding and body condition (Belanger & Bedard 1990, Evans & Day 2001, Jamieson et al. 2006, Casas et al. 2009), any decrease in breeding success (Bety et al. 2003) or any long-term population decrease (Brochet et al. 2009).

However, even if hunting disturbance impacts on populations, populations may respond through density-dependent negative feedback mechanisms (e.g. Aebischer 1997, Connelly et al. 2012), and thus a population may not decrease until a certain level of disturbance has been reached (see Fig. 1). Moreover, sustainable hunting can only be achieved by reducing populations to take advantage of the density-dependent increase in survival or breeding output, resulting in lower population size, but in higher sustainably harvested yield (Sutherland 2001). Thus, reduction in the distribution of a species within a specific site should not always be considered a significant disturbance impact causing long-term population decrease *a priori*. Statements like "Any event which contributes to the reduction of the size of the habitat of the species within the site can be regarded as a significant disturbance" of the European Commission (2001) should therefore be reexamined.

Hunting disturbance and harvest should not be regarded as independent from each other. The trade-off between disturbance tolerance and harvest permits a better understanding of hunting influences on hunted birds, because avoidance of hunters may cause disturbance but also decreases the harvest rate (see Table 1). Moreover, we found that the most intolerant species to hunting disturbance in Hellas tend to be the most numerous, except for the gadwall, which is less numerous (Birdlife International 2004, Kazantzidis et al. 2007, Thomaides et al. 2011). Therefore, migratory hunted bird species in Hellas appear to be adequately able to compensate for potential hunting disturbance impacts.

For effective conservation and management programmes, disturbance from all factors (e.g. aircraft, walking and farming), not just hunting, should be managed for migratory quarry species (Harradine 1998, Blanc et al. 2006, Dooley et al. 2010). Thus, reductions in disturbance should be a routine part of management. Management goals could include a desirable distribution of quarry species for the benefit of hunters, farmers and birdwatchers, and if a species is intolerant to disturbance and suffer a high harvest, then detailed legislative guidelines and directives should be issued, and a hunting impact assessment study should be carried out.

We conclude that hunting management should not be based upon generic legislative guidelines, as is attempted in some cases (for example staggered closing dates due to prenuptial bird migration and hunting prohibition in protected areas through the EU Birds and Habitats Directives). High diversity in biological factors and socio-economic needs require local management supported by multidisciplinary experts, advisory information and monitoring.

Our suggested diagnostic procedure (see Table 1) is based on factors which can be assessed with reasonable accuracy from the literature (nocturnal feeding ability and food preferences), field observations (flock size, food and habitat availability and predators) and local management and monitoring (refuges, hunting and harvest). Thus, the procedure will provide a useful and robust tool that can help managers in evaluating the susceptibility of a species or group of species to hunting disturbance at a regional or flyway level depending on the desired accuracy and data availability. However, this procedure should not be considered as the final index on which hunting management should be based. Some modifications may improve the procedure in other areas outside Hellas, making it more effective under local conditions.

The diagnostic procedure could guide legislation for wise hunting practices; hence, management measures could be evaluated and implemented more effectively, distinguishing and giving priority to the most intolerant species. In detail, the first three factors are related to bird behaviour so any management measure to decrease disturbance is impossible. The next three factors are related to ecology. For example, if a species is food-limited, hunting disturbance can be decreased with food provision management measures (Henderson et al. 2004, Ma et al. 2010). If habitat availability is limited, hunting disturbance can be decreased through conservation and creation of suitable habitat (Sorrenti & Concialini 1996, Lecocq 1998).

The last three factors are related to hunting management. To mitigate hunting disturbance through hunting management, the most effective management approach has been to establish refuge areas (Fox & Madsen 1997, Bregnballe et al. 2004, Dooley et al. 2010). Creating refuges will help retain a nucleus of migratory birds in the area to provide opportunities for hunting (Giroux & Bédard 1988), and in some cases hunters self-regulate their activity (Schou & Bregnballe 2007). Dooley et al. (2010) found that after disturbance mallards moved within < 10 km, usually < 5 km, and they proposed the establishment of a refuge at this geographic scale.

The minimum diameter of a refuge should be three times the escape flight distance of the species (Fox & Madsen 1997). Some authors suggested that refuges should be at least 1.47-2 km^2 (Giroux & Bédard 1988, Belanger & Bedard 1990). Establishing a buffer zone between hunting and foraging areas has been proposed by Holm et al. (2011) for preventing displacement of coots.

Mobile hunting activity is more disturbing than hunting from fixed points (Fox & Madsen 1997). One or two mobile shooting punts reduced wigeon numbers, whereas numbers were unaffected by the presence of up to 4-6 stationary punts (Madsen 1998a).

Temporal restriction of hunting should be considered from 1-2 days until few weeks (Fox & Madsen 1997, Madsen 2001a, Bregnballe et al. 2004, Bregnballe & Madsen 2004, Dooley et al. 2010). In a recent study with radio-marked mallards, Dooley et al. (2010) found that 1-2 days of protection from hunting was adequate for mallards to recover. Moreover, appropriate statutory hunting suspension during cold spells of prolonged periods is recommended, especially for waterbirds and ground-feeding birds. Integrated management should also consider human dimensions of hunting, including local traditions and economic benefits (Mathevet & Mesléard 2002, Mattsson et al. 2007).

Some issues that require additional research are: 1) the relation between hunting disturbance and physiological and reproductive parameters of individual birds, 2) the relation between hunting harvest, disturbance and hunting pressure, 3) the relation between hunting and predator disturbance and 4) the evaluation of harvest and disturbance factors of Table 1. New tracking technologies can relay information from sensors that provide data about the physiology and activities of disturbed migratory birds (Bridge et al. 2011).

Mathematical and statistical modelling methods could be useful to confirm some of the statements presented in this paper (Ross 1996, Howard 2007). A possible modelling approach could include the observation of bird species movements from one site to another, the holding and the waiting times at each site, the construction of stochastic models based on semi-markov chains and the prediction of the long-term probabilities to be at each site under hunting pressure (Howard 2007). Other sophisticated models could be used to examine if there is any critical threshold at which disturbance can have additive impacts that cause long-term population decrease. Goss-Custard et al. (2006) and Liley & Sutherland (2007) give examples of such models for wading birds.

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