Hunting vulnerability and wintering strategy among waterfowl in Camargue, France

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Source: Wildlife Biology, 4(1) : 13-21

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1998.011

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Dehorter, O. & Tamisier, A. 1998: Hunting vulnerability and wintering strategy among waterfowl in Camargue, France. - Wildl. Biol. 4: 13-21.

Hunting vulnerability of waterfowl species has often been associated with age and sex classes, or with body condition in relation to physiological constraints. In the Camargue, southern France, body weights and daily feeding duration of three dabbling duck species (teal *Anas c. crecca*, gadwall *A. strepera* and wigeon *A. penelope*) have recently been used to isolate three main periods in the winter season (August to March). These periods are characterised successively by high, low and high levels of energy demand, and they constitute the time schedule for a model of wintering strategy. For feeding, birds exploit the productive hunted marshes, mostly during the periods of high energy demand. In this study, we tested the hypothesis that hunting vulnerability can be predicted from these seasonal patterns, being highest when energy demand is highest (at the beginning and at the end of the winter), and being lowest in mid-winter when energy demand is lowest. We used numbers of birds killed (45,000 birds, including the species mentioned above, as well as mallard *Anas platyrhynchos* and coot *Fulica atra*) collected from hunting bags in three locations over 12 years, validated on 110,000 killed birds from another location, and adjusted to living (censused) birds. The results do not fit exactly to our predictions. They rather suggest that hunting vulnerability results from a combination of energy demand, habitat selection (both related to wintering strategy), chronology of migration and trophic status of duck species (granivorous vs herbivorous). At the beginning of the winter season, granivorous species, the first to arrive, are inexperienced to hunting, have a high energy demand and are highly vulnerable. At the middle of the winter season, when energy demands are low, the birds can escape from hunting to refuge areas. Meanwhile, herbivorous species, still arriving, must spend more time on feeding (vegetative food contains less energy than seeds) on productive hunted marshes; they suffer high hunting vulnerability from hunters who shift from granivorous to herbivorous species. At the end of the winter season, granivorous and herbivorous species rely on hunted areas for feeding and are very vulnerable. However, hunting vulnerability of a given species is lowered since hunting pressure during that last period of winter is shared among a maximum number of game species, some of which are migrating back from Africa.

Key words: Camargue, energy demand, hunting, vulnerability, waterfowl, wintering strategy

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Received 6 May 1996, accepted 9 October 1997

Associate Editor: Hannu Pöysä

Winter survival is a major component of population dynamics, especially for game species for which relationships between hunting mortality and natural mortality are complex (Anderson & Burnham 1976, Nichols, Conroy, Anderson & Burnham 1984, Montalbano, Johnson, Miller & Rusch 1988, Nichols 1991a). The effect of hunting on winter survival is particularly important in Europe where hunting pressure is much higher than in North America (Scott 1982, Tamisier 1985a), and hence additive mortality is more likely to occur (Owen & Black 1990). However, hunting is not an easy factor to manipulate (Bell & Owen 1990) and its two main components, direct mortality and disturbance, can have cumulative effects on population size and distribution (Frederick, Clark & Kaas 1987, Ebbinge 1991, Madsen 1995). The first component (direct mortality related to hunting) will be analysed in this paper. Several factors increase vulnerability to hunting. For instance, birds in poor body condition were found to be more vulnerable to hunting (e.g. Greenwood, Clark & Weatherhead 1986, Hepp, Blohm, Reynolds, Hines & Nichols 1986, Dufour, Ankney & Weatherhead 1993). Likewise, McNamara & Houston (1987) suggested that birds are presumably more vulnerable to hunting if they have higher energy demands. Energetic requirements of a given species vary from month to month during the winter and have led to models describing alternative wintering strategies for ducks (Heitmeyer 1985, Allouche 1988). In the Camargue, south France, variations in daily feeding duration and body weights of three dabbling ducks (teal *Anas c. crecca*, gadwall *A. strepera* and wigeon *A. penelope*) allowed the identification of three successive periods (of 2-3 months each) of high, low and high energy demand during the winter season (Tamisier, Allouche, Aubry & Dehorter 1995). During the first period, migrating birds, which are mostly juveniles, arrive and feed intensively until maximum weight is achieved. During the second period (October - December), birds disposing of nutrient reserves can spare energy and time for activities other than feeding and sleeping. During the third period, birds must store new reserves for migration and future reproduction, so they feed intensively. These three periods are considered the time schedules of the Camargue model of wintering strategy (Tamisier et al. 1995). During the periods of longest feeding times (periods one and three), birds select the most productive areas among those available in the Camargue which also are the most heavily hunted places (Tamisier & Grillas 1994, Dehorter & Tamisier 1996). During the central period of the winter season when feeding duration is shortest, birds select more protected areas.

Thus energy acquisition and conservation strategies occur at the expense of increased risk of getting killed (Tamisier et al. 1995); but the periods of high, low and high energy demand might in turn lead to seasonal variation in vulnerability to hunting. We therefore predict highest hunting mortality at the beginning and at the end of the winter season when energy demand is highest, falling to a minimum during mid-winter when energy demand is lower. In this paper, we test the prediction by analysing hunting bags collected in the Camargue where hunting pressure is consistently very high over a non-stop 7.5-month season.

Study area and methods

The Camargue, a deltaic area at the mouth of the Rhone river on the Mediterranean sea, comprises over 85,000 ha of fresh, brackish and salt-water marshes of which 19,000 ha are protected by law. It is the most important wintering site for ducks in France (Rüger, Prentice & Owen 1987). Birds arrive in August and begin to depart in January. Based on monthly aerial censuses from 1964/65 to 1993/94, mean maximum numbers of ducks occur in December (mean = 115,207; SD = 30,272) and mean maximum numbers of coots *Fulica atra* occur in November (mean = 29,172; SD = 8,933) (unpubl. data). Most of these birds breed in central and eastern Europe (Cramp & Simmons 1977), although both mallards *Anas platyrhynchos* and coots breed locally; their numbers peak during September-November. Outside protected areas, waterfowl hunting occurs everywhere in the Camargue, both on private properties (mostly on Saturdays and Sundays) and in public areas (usually every day). Total bags have been estimated from random sampling using questionnaires (Anonymous 1976, Trolliet 1986) and by direct collection of hunting bags (Tamisier 1987). About 150,000 ducks and more than 50,000 coots are killed every year. Hunting on 40,000 ha of privately owned fresh marshes kills about 100,000 ducks per year; hunters operating on 5,000 ha of public freshwater areas and, to a lesser extent, on 25,000 ha of salt marshes, kill about 50,000 birds per year (Tamisier 1987). The apparent discrepancy between dead and

live (censused) birds comes from the cumulative nature of the bags throughout the hunting season compared to the instantaneous counts, suggesting a high turnover of transient birds moving elsewhere (Pradel, Rioux, Tamisier & Lebreton 1997). The size of the hunting bag suggests a very high level of hunting pressure in the Camargue.

Two sets of hunting bags differing in the availability of data were analysed separately. The first set concerned three private properties (A, B and C), located in the eastern, central and western part of the Camargue. These properties were selected because of the availability of specific monthly hunting bags for 12 years, between 1965/66 and 1981/82. Together they account for a total of ca 25,000 ducks and 20,000 coots killed during the 12-year period. The second set concerned a fourth private propriety in central Camargue (D) where data were available for 10 consecutive years only (1973/74 - 1982/83). The bag accounts for a total of ca 96,000 ducks and 14,000 coots. Hunting bags from private properties differ from those of public hunting areas in terms of species composition, size and chronology (Tamisier 1987). Consequently, our results can only be applied to hunting on private properties, representing about two thirds of the total bag of the Camargue.

The hunting season started for all waterfowl species in mid-August in the largest eastern part of the Camargue, and in mid-July in the west. It closed for all species except mallard at the end of March from 1965 to 1973, on 11-23 March from 1974 to 1980, and on the last day of February in 1981. For mallard, the hunting season closed in mid-February each year. In order to standardise months and years, we only analysed data from September to February. Hunting is allowed from two hours before sunrise to two hours after sunset. Living decoys (mallards) are commonly used and there is no bag-limit. Hunting pressure, defined in terms of density of hunters over the Camargue and numbers of hunting-days per week is considered constant during the hunting season, although there are no data to document this. Poaching (i.e. hunting at night, outside the hunting season and/or on protected areas) is generally considered not to be significant in the Camargue (pers. obs.). Duck hunting in the Camargue is mostly based on crepuscular movements of birds between open wetlands where they mostly rest and sleep at day, and shallow marshes (2-20 km away) where they feed at night. This spatio-temporal distribution is considered a fundamental life trait of wintering ducks, rather than a recent adaptation to hunting disturbance (Tamisier 1985b, McNeil, Drapeau & Goss-Custard 1992). Most ducks rest on protected areas. Conversely, about 90% of ducks feed at night in hunted places where water management practices (pumping of freshwater) increase plant productivity (Tamisier & Grillas 1994, Dehorter & Tamisier 1996), and enhance food availability (Pirot, Chessel & Tamisier 1984). Herbivorous duck species require longer feeding periods than granivorous duck species to satisfy energetic demands, and hence are more dependent on the rich freshwater marshes where they must feed partly by day. So, in addition to crepuscular flights, they also commute by day between the protected resting areas and the hunted feeding places (Campredon 1981). Hunters take advantage of these diurnal movements as well as of the diurnal presence of the herbivorous duck species on their marshes.

Coots make no regular flights, feeding by day on lakes and marshes where they sleep at night along the borders (Allouche, Dervieux, Lespinasse & Tamisier 1990a, Allouche, Dervieux & Tamisier 1990b). They are killed either opportunistically or during special hunting parties called 'battues': coots which gather naturally in huge numbers and usually are reluctant to fly, are 'driven' slowly (i.e. forced to swim) by hunters using boats until they flush and can be killed by the hundred. Traditionally, both ducks and coots exploit the same feeding and resting areas during the winter season. As a rule, hunters have no species preference among ducks, but they definitely prefer ducks to coots (pers. obs.).

We analysed data on coots and four dabbling duck species, three of which are herbivorous species (wigeon, gadwall and coot) and two of which are granivorous species (mallard and teal). Collectively, these species represent ca 75% of the total bag of ducks and coots in the Camargue and ca 80% of the censused population. We used analysis of covariance (ANCOVA) with GLM procedure (SAS Institute Inc. 1985) to evaluate numbers of killed birds in relation to the stage of the winter season (six months). The number of birds censused in the Camargue during the same years was entered as the covariate to eliminate the effect of population size (see Table 2, Figs 1 and 2). The reliability of such census data has been confirmed previously (Dervieux, Lebreton & Tamisier 1980). When necessary, number of birds and hunting bags were log-transformed to normalise the distribution and homogenise variances. We used combining probability procedures to combine the statistical

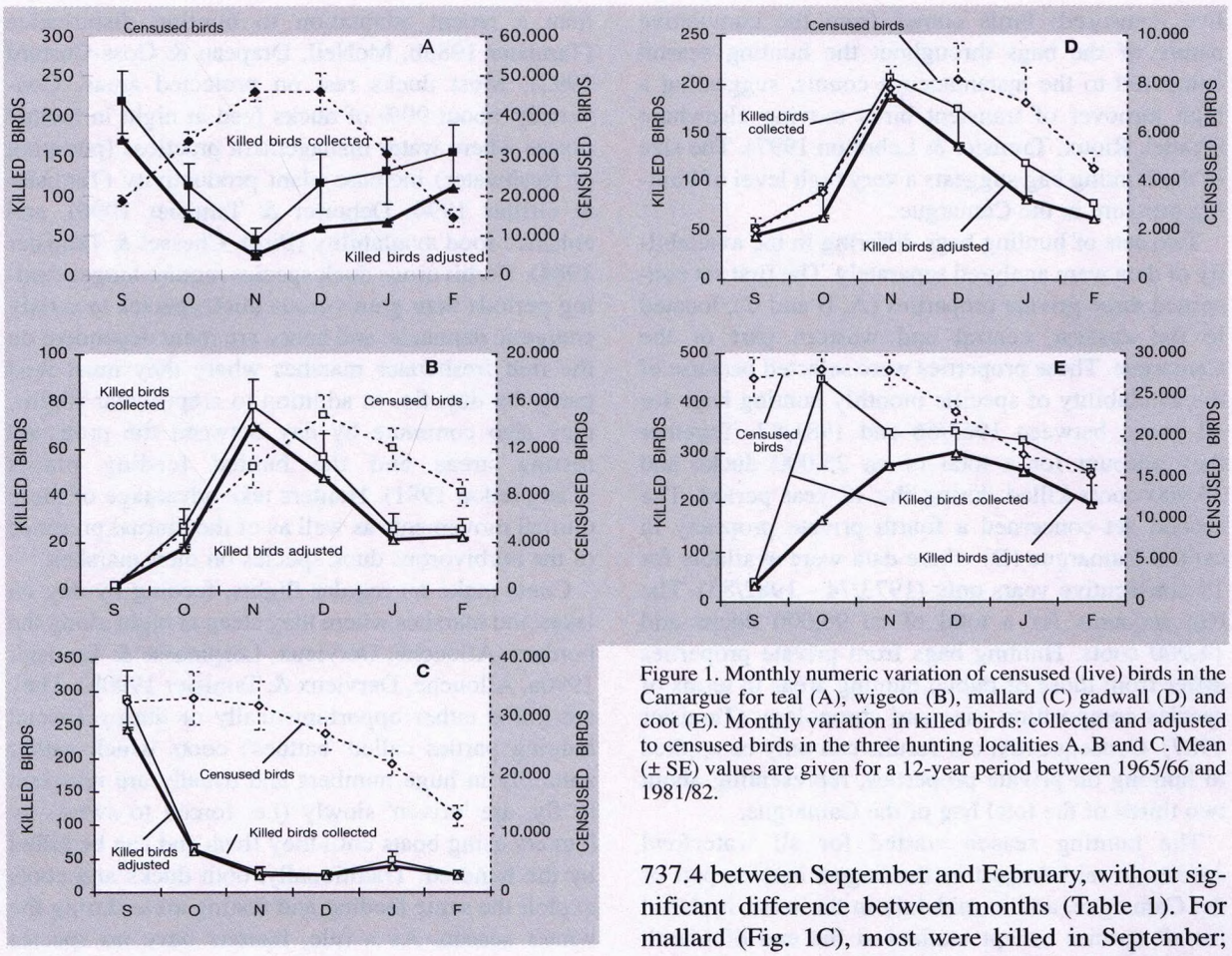

Figure 1. Monthly numeric variation of censused (live) birds in the Camargue for teal (A), wigeon (B), mallard (C) gadwall (D) and coot (E). Monthly variation in killed birds: collected and adjusted to censused birds in the three hunting localities A, B and C. Mean (± SE) values are given for a 12-year period between 1965/66 and 1981/82.

results from localities A, B, C and D, according to the formula $-2 \sum \ln p_i$, where p_i is the probability level for the i^{th} locality (see Table 2) (Sokal & Rohlf 1981). Hunting vulnerability was estimated as the number of killed birds adjusted to the number of censused birds.

Results

At localities A, B and C, the monthly mean number of killed birds of all species ranged from 540.6 to 737.4 between September and February, without significant difference between months (Table 1). For mallard (Fig. 1C), most were killed in September; afterwards, numbers killed were very low with no major monthly fluctuations between October and February. For teal (Fig. 1A), the curve revealed a parabolic pattern, with minimum kill values occurring in November. Conversely, for gadwall and wigeon and, to a lesser extent, for coot, maximum values occurred in November (October for coot). For all species, there was no relationship between the number of birds present in the Camargue and the number killed in the same month (Table 2). The monthly variation of mallard (see Fig. 1C) was highly significant, September values differing significantly from all other months; October also differed from

Table 1. Monthly mean (± SE) number of ducks (mallard, teal, gadwall and wigeon) and coots killed over a 12-year period during 1965/66-1981/82. Multiple comparison tests were carried out on log-transformed numbers. Identical letters indicate non-different means.

	Sep	Oct	Nov	Dec	Jan	Feb
Ducks killed	538.6 (83.0)^a	289.3 (56.2)^a	354.0 (37.3)^a	380.8 (56.9)^a	312.3 (64.2)^a	279.1 (46.8)^a
Coots killed	38.5 (11.0)^a	448.1 (196.3)^b	342.1 (69.7)^b	343.6 (61.7)^b	324.5 (77.9)^b	261.5 (67.0)^b
Total birds killed	577.1 (86.7)^a	737.4 (203.6)^a	696.1 (78.7)^a	724.4 (93.0)^a	636.8 (97.2)^a	540.6 (74.5)^a

Table 2. Monthly effects (ME), combined probability of localities A, B, and C vs D at probability level P (CP), covariable effects (CE), and multiple comparisons month by month for localities A, B and C (MP). Identical letters indicate non-different monthly values.

		ME			CP		CE			MP					
Species	Loc.	F	d.f.	P	-2∑ln p	P	F	d.f.	P	S	O	N	D	J	F
Mallard	ABC	22.99	5, 59	0.001	47.787	0.001	0.306	1, 59	0.582	a	c	b	b	bc	b
	D	1.24	5, 46	0.306			0.91	1, 46	0.340	a	b	b	b	b	ab
Teal	ABC	1.982	5, 62	0.187	12.296	0.05	0.128	1, 62	0.722	a	a	b	ab	ab	a
	D	5.66	5, 52	0.003			2.79	1, 52	0.101	a	b	b	b	ab	ab
Gadwall	ABC	6.56	5, 62	0.001	19.671	0.001	3.997	1, 62	0.05	a	ab	c	c	b	ab
	D	4.23	5, 53	0.0026			4.65	1, 53	0.036	a	ab	c	c	b	ab
Wigeon	ABC	18.588	5, 64	0.001	39.991	0.001	0.056	1, 64	0.814		a	b	b	ac	ac
	D	3.6	5, 52	0.0072			0.41	1, 52	0.526	a	a	bc	b	bc	ac
Coot	ABC	7.553	5, 59	0.001	24.77	0.001	0.140	1, 59	0.710	a	b	b	b	b	b
	D	2.57	5, 53	0.0372			0.01	1, 53	0.904	a	ab	b	ab	a	ab

November, December and February. For teal (see Fig. 1A), the monthly variation was not significant. For wigeon and gadwall, values of November and December were homogeneous and differed significantly from the other months (see Fig. 1B,D). For coot, values of November to February were equivalent and differed significantly from September (see Fig. 1E).

At hunting location D, the monthly variation of birds killed resembled that of localities A, B and C for all species. There was no covariable effect, except for gadwall (see Table 2); there was an inverse relationship between the number of gadwalls present and the number killed (slope estimate = -0.02). For teal, the monthly variation is significant (see Table 2) and multiple comparisons showed November to be significantly different from September and February (Fig. 2). Hence combining probabilities were applicable. This procedure increased the robustness of the results, especially for teal (see Table 2).

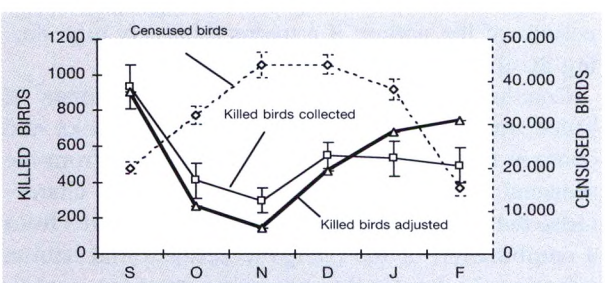

Figure 2. Monthly numeric variation of censused (live) teal in the Camargue. Monthly variation in teal killed in hunting locality D: collected and adjusted to censused teal (compared with Figure 1A). Mean (± SE) values are given for a 10-year period (1973/74-1982/83).

Discussion

At localities A, B and C, and within some limits at locality D, the number of birds killed for all species pooled is not dependent on the number of censused birds. In Canada, an inverse relationship between killed birds and live birds has been demonstrated for three duck species (Hochbaum & Walters 1984). At the species level, and independent of the size of the censused population, hunting vulnerability in the Camargue, like in California (Miller, Beam & Connelly 1988), varies according to month and according to species. But in contrast to our original prediction, monthly patterns of vulnerability do not directly fit with variations in energy demand. Several parameters are likely to covary with month and each needs to be discussed separately at the level of species or group of species. Juveniles, which are usually the most numerous individuals in autumn when the hunting season starts, are known to be more vulnerable to disturbance (Martin & Carney 1977, Miller et al. 1988), and usually have lower survival rates than adults (Johnson, Nichols, Conroy & Cowardin 1988, Owen & Black 1990, Nichols 1991b). Moreover, birds, independent of age, are known to be more vulnerable to a given mortality factor when they experience it for the first time (Hochbaum & Walters 1984). Even if birds learn rapidly to avoid predators (e.g. hunters), they apparently 'forget' rapidly too (Hochbaum & Walters 1984). Thus, after several month without exposure to hunting, ducks have to reexperience hunting before it affects their behaviour. This is true for resident mallards as well as for migrating teals that have not yet experienced high

hunting pressure between their Siberian breeding grounds and the Camargue (Lampio 1983). Consequently, the high vulnerability to hunting of mallard and teal in September can at first be interpreted as the result of the cumulative effects of the abundance of juveniles and inexperienced birds at this period of the year. Similar results were obtained for both species in Great Britain (Harradine 1985), and for green-winged teal *Anas crecca carolinensis* and mallard in Canada (Hochbaum & Walters 1984) and the USA (Miller et al. 1988). From the data available, it is not possible to isolate a specific juvenile effect from the lack-of-experience effect, but we can estimate that the lack-of-experience effect lasts about 1-2 months. The other species arriving later have experienced hunting pressure before reaching the Camargue. The case of coots will be analysed separately.

Hochbaum & Caswell (1991) showed that for resident mallards, the number of birds killed is positively correlated with the number of adults still moulting their wing feathers. In the Camargue, the last juveniles to fledge are observed in mid-September (Isenmann 1993), when the latest breeding females should be in moult. For these birds at least, incomplete or late moult probably adds to juvenile and lack-of-experience effects to increase hunting vulnerability of mallards early in the hunting season.

A major difference in hunting vulnerability during the three main periods of the winter exists between granivorous (mallard and teal) and herbivorous duck species (gadwall and wigeon). Granivorous ducks exhibit the lowest vulnerability in mid-winter, whereas this occurs at the beginning and at the end of the winter for herbivorous species. If we assume that hunting pressure is constant throughout the winter, and that hunters have no preferences for specific duck species, maximum hunting of granivorous species when the season starts can be related to two points. First, granivorous species occur in higher numbers at that time (they represent 94 and 87% of the duck community in September and October vs 66 and 63% in January and February), and secondly they have high energy demands, so they depend on productive marshes for feeding (which also are the hunted marshes) (Tamisier et al. 1995, Dehorter & Tamisier 1996). As the winter season proceeds, granivorous species have shorter feeding periods and may stay throughout the day on protected areas; crepuscular flights between protected and hunted areas occur when it is completely dark, hence avoiding hunting. Moreover, they become increasingly aware of hunting. Meanwhile, herbivorous ducks become more and more numerous. These ducks have longer feeding periods per day than granivorous species since vegetative parts have a lower energetic value than seeds (Paulus 1988, Tamisier et al. 1995). Consequently, they spend much more time than granivorous species on the productive hunted marshes where they must feed partly by day (Campredon 1982, Allouche 1988). Therefore, they have a higher risk of being killed. At the end of the season, all species in the Camargue have high energy demands (Tamisier et al. 1995); granivorous species join herbivorous ones to feed intensively on the hunted marshes, and they scatter on hunted shallow zones (Pirot et al. 1984) by late winter. Since the probability of being killed is inversely correlated with the size of a group of ducks (Hochbaum & Walters 1984), scattering at the end of the season increases hunting vulnerability.

Coot react differently to hunting. They are not killed in September when their numbers are at a maximum, when they are hunting inexperienced, and when they have high energy demands (Allouche 1988). From the start of the hunting season until September, hunters selectively shoot ducks which are vulnerable and occur in sufficient numbers. From October to December-January, when granivorous ducks become less abundant on the hunting sites, and when hunters shift towards herbivorous species, coots are killed either occasionally or through 'battues' where several hundred birds can be collected locally in a few hours. At the end of the season, when coots must store reserves (Alisauskas & Ankney 1985, Allouche 1988) and when many scatter to start breeding (Allouche 1988), they remain vulnerable to hunting. So hunting vulnerability of coots seems to be inversely related to the vulnerability of granivorous duck species during the first two periods of the winter; it remains relatively high during the third period of the winter season.

Conclusively, vulnerability (i.e. the number of killed birds adjusted to living birds) of ducks and coots in the Camargue cannot be predicted from the seasonal changes in energy demand which characterise the local wintering strategy only. It results from a combination of the energetic demand and habitat selection (both related to wintering strategy), experience with hunters, phenology and trophic status (granivorous vs herbivorous). During the first period of the winter season, the few birds present cumulate all parameters of vulnerability and suffer the highest

mortality. During the mid-winter period, granivorous duck species can avoid being hunted by using refuge areas which are unsaturated (Taylor 1984, Frontier & Pichot-Viale 1995). Conversely, herbivorous duck species rely much more on the productive hunted marshes because they need more time to meet their energy demand at all months of the period. They have no way of escaping to protected zones and suffer the highest hunting vulnerability at mid-winter when they are the only species exploiting the hunting marshes. At the end of the winter season, granivorous and herbivorous species have higher energetic demands and need to exploit the productive hunted marshes. Hunting pressure is shared by all species of ducks and by coot, and also by several migrating bird species arriving from Africa (garganey *Anas querquedula*, pintail *A. acuta* and many shorebird species). Hence hunting of a given species is lowered, which partly explains why hunting vulnerability is rather low during that period. Among granivorous species, the higher vulnerability of teal may be associated with differences in breeding distribution. Teal breed in Siberia, whereas mallard breed either locally or in central Europe (Cramp & Simmons 1977); hence teal probably must store more energy than mallard before leaving the Camargue to cope with a much longer migration route and with worse conditions on the breeding grounds. Coots appear to be considered an alternative prey to granivorous species by hunters, at least during the first two periods of the winter; however our data only show a simultaneity of events.

Our results have some management implications. They illustrate that during the first and last periods of the winter season, birds are hunted while they experience severe natural constraints. Thus a reduction of the length of the hunting season, e.g. by setting a later opening date and an earlier closing date, would avoid exacerbating these constraints. But, delaying the opening date would not lower the size of hunting bags of the first days or weeks of the hunting season before ducks experience hunting. Conversely, restricting the hunting season to a period when birds have the least energy demands, i.e. during the middle part of the winter season (October to December or January), would be beneficial to them as compared to the present situation. We put forward the hypothesis that the benefit would be higher for the granivorous duck species than for herbivorous species, since the former are less dependent on the productive hunting marshes. Furthermore, since hunting vulnerability of waterfowl seems ultimately associated with energy demand, and since waterfowl in the Camargue rely on hunted marshes for feeding, a status of protection of part of these marshes would be beneficial to the birds, provided management practices of the marshes are maintained after protection. Thus, ducks and coots in these areas could safely meet their energetic requirements, would gain improved body condition before leaving the Camargue and would have a higher probability of increasing their breeding success.

Acknowledgements - we wish to thank all the hunters who kindly allowed us to gather the requested hunting bags. We also thank Dr. A. Caizergues, M. Lambrecht and J.-D. Lebreton for helpful criticisms on a previous draft, and Dr. James Aronson for the English revision of our manuscript.

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