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How does harvest size vary with hunting season length?

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Manipulating hunting season length is often used as a population management tool but the effects of these changes on total harvest have rarely been studied. We modelled relative changes in national annual bag size as a function of relative change in hunting season length in 63 cases involving 28 species in Denmark (1957–2007). The duration of the hunting season, initially lasting 30–365 days, was modified to 39–204% of the former length. The undifferentiated effect of season length change on bag size change (all 63 cases) was not statistically significant ($b = 0.16$, 95%CI: -0.04 – 0.36), with a 10% (95%CI: -3 – 22 %) predicted decrease in bag size upon a 50% reduction of season length. However, the functional relationship between the relative change in bag size and the change in season length differed between sedentary and non-sedentary species and interacted with the motivation behind changing season length (population management/ethical/other). In non-sedentary species, changes in bag size correlated positively with changes in season length (overall response: $b = 0.54$, 95%CI: 0.14 – 0.95): reducing the hunting season to 50% of its initial length would on average result in a 31% reduction (95% CI: 9 – 48 %) of total bag size. This overall effect interacted with the motivation for season length changes, being strongest for ‘other reasons’ (mainly harmonization of hunting periods for related species) but was absent when seasons were changed for reasons of ‘population management’. In sedentary species, changes in season length had no effect on bag size. Our results suggest that manipulating hunting seasons of duration ≥ 1 month by less than 50% is generally inefficient as a means of predictably changing harvest rates. This may be because recreational hunters either invest a fixed effort or aim for a specific yield within a given season, neither strategy being affected by changes in hunting seasons.

Manipulating the length of the hunting season has been a widely used population regulation tool in wildlife management (Sinclair et al. 2006), but its effect on population dynamics is largely unknown and difficult to predict for several reasons (Kokko 2001). Firstly, a hunter’s total kill is not necessarily proportional to season length, as the relationship between hunters’ effort and the number of days available to hunt is affected by many motivating factors (Peterson 2001, Schwabe et al. 2001, Willebrand et al. 2011). Secondly, the effect of changes in harvest rates on total mortality and population growth rates depends on the extent to which hunting-induced mortality is additive or compensatory (Sutherland 2001, Sandercock et al. 2011), which also may relate to seasonal timing of the harvest (Palmer and Bennett 1963, Kokko 2001, Brøseth et al. 2012). Hunter efficiency may also be seasonally dependent on weather conditions or migration phenology (Merkel 2010). Finally, variation in length and timing of hunting seasons may influence populations through various non-lethal effects related to the disturbance caused by hunting activities (Fox and Madsen 1997, Dooley et al. 2010).

The basic premise for regulating harvest rate through the length of the hunting season is that the duration of the hunting season constrains in some way the hunters’ total number of game bagged. Hence, if all other factors are equal

(i.e. controlling for effects of seasonality or decrease in hunting success due to depletion of game stocks or disturbance effects), a change of the season length should only be associated with a similar change in the number of game bagged if hunters’ daily killing effort is constant over the season and unrelated to its length. On the contrary, hunters may aim to achieve a fixed total hunting bag or invest a constant effort (e.g. three one-day hunting trips per season) per season. This may be motivated by satisfying a recreational need or because hunters with exclusive hunting rights to a delimited area do not wish to overharvest their ‘private’ stock. Either way, such hunters would be more likely to adjust their daily effort in response to variation in the season length to achieve their desired harvest level, so long as a sufficient ‘time buffer’ remains within the season to enable them to do so. For this type of hunter, a change in the length of the hunting season should not result in a similar relative change in the total number of quarry bagged, or in any change at all, unless the length of the season is sufficiently shortened to constrain their killing effort to a level that falls short of achieving their fixed goal. While subsistence hunters maximise their individual yield from a common population in relation to opportunities (e.g. native peoples in Greenland: Merkel 2010), recreational hunters in modern societies may harvest in a way that achieves a fixed yield

or fixed effort (Joensen 1974, Peterson 2001) although their hunting effort to some extent may be influenced by the number of days available (Schwabe et al. 2001).

Several North American studies have provided evidence for hunting season length affecting seasonal harvest size and/or harvest rate amongst recreational hunters, for open seasons lasting less than 30 days (Heusmann and McDonald 2002, Norman et al. 2004, Fleskes et al. 2007, Chamberlain et al. 2012). Much less information exists on the effects of changes of hunting seasons lasting for more than one month, as is the case for most national hunting seasons currently operating in many European countries. Nevertheless, for several species with trans-national flyway populations, regulation of national hunting seasons is one of the few harvest management regulatory mechanisms available to European statutory agencies.

In this paper, we aim to determine the extent to which harvest size is sensitive to changes in length of the open hunting season, based on data from a western European country (Denmark). To establish relationships between changes in national hunting season length and national harvest rates, we analysed changes in bag size based on data from Danish hunting statistics. We identified 63 periods relating to 28 species where changes in the hunting season could be related to changes in the annual bag size before and after the change. Because Danish hunting regulation has never involved the application of bag limits, the Danish hunting bag statistics offer an exclusive opportunity to assess how general changes in the timing or length of the hunting season may affect bag size on a large geographical scale.

Materials and methods

Data

Since 1941, all Danish hunters must report their annual kill of different game species at a county (since 2006 at a municipality) level. During the open season, hunters holding a valid national hunting license, with permission from the landowner, may kill an unrestricted number of game, including ungulate species (there being no local or regional quotas or bag limits). Excepting a very few species-specific regulations on small islands of negligible size (< 100 km²) compared to the total land surface (43 093 km²) of the country, hunting season durations are the same throughout the country. Hunting seasons are determined by parliament and subject to regular revision based on advice from the national Wildlife Management Board, an advisory panel of non-governmental organisations (e.g. Danish Hunter's Association, landowner organisations, nature conservation and animal welfare organisations).

Analysis

From the annual Danish bag statistics, 1941–2010, we distinguished 63 changes in hunting season length (1957–2007) relating to 28 game species, for which national bag data existed before and after the change (Table 1). In 11 cases, different population segments were subject to

different hunting seasons (e.g. males and females) but as these different segments were not specifically discriminated in the bag, we used the average length of the hunting season among all groups as measure of hunting season length.

For each case, we estimated the log₁₀-transformed bag size (log[B]) from five years before to five years after the change in hunting season as:

$$\text{Log}[B] = b_0 + b_1X_1 + b_2X_2 + b_3X_1X_2$$

where X_1 is an indicator variable for the before and after each situation ($X_1 = 0$ for before season length change and $X_1 = 1$ for after the season length change) and b_1 is the coefficient of the relative difference in bag size as a result of the change; X_2 is the year (linear covariate) and b_2 and b_3 are the coefficients for yearly trends in bag size before and after the hunting season change respectively. From this model, we derived the relative, trend adjusted change in bag size concurrent with the season length change, $\Delta\log[B] = \log[B]_{\text{after}} - \Delta\log[B]_{\text{before}}$, as the least square means difference between the model's estimates of log[B] before and after the season length change in the 1st year after the change in hunting season. We used this method, because it accounts for different long-term trends in bag size before and after the hunting season change (five years on each side), which could be caused by different population growth rates because of a changed hunting pressure. Under all circumstances, the estimate of $\Delta\log[B]$ obtained with the described method was highly correlated with the simple difference in bag size in the season before (t) and the season after ($t+1$) the change in hunting season ($\Delta\log[B]_{(t+1)/(t)} = \log[B]_{t+1} - \log[B]_t$; linear regression: $\Delta\log[B] = 0.9944\Delta\log[B]_{(t+1)/(t)} + 0.0074$, $r_{61}^2 = 0.882$).

For each of the 63 cases, we tested the statistical significance of $\Delta\log[B]$ as the ratio between the coefficient and its SE, which was t -distributed with $n - 4$ DF, where n is the number of years with bag size data (i.e. DF = 6 if bag size data existed for all five years before and after the change in hunting season length).

We measured the relative change in hunting season length as the differences between the log₁₀-transformed hunting season lengths before and after regulation of season length ($\Delta\log[SL] = \log[SL]_{\text{after}} - \log[SL]_{\text{before}}$).

In the analyses of overall relationships between hunting season length and annual bag size, we regressed $\Delta\log[B]$ against $\Delta\log[SL]$ for the entire dataset. A priori, we predicted that if hunter efforts were limited by the length of hunting season $\Delta\log[B]$ should correlate positively with $\Delta\log[SL]$. If the total bag size was directly proportional to the length of the hunting season, a relative change in hunting season length should result in a change of similar magnitude in bag size, which in turn should result in a slope of 1 in the power function of $\Delta\log[B]$ on $\Delta\log[SL]$. If total bag size was constant regardless of hunting season length we would predict a slope of 0. Intermediate responses between these two extremes should result in a slope between 0 and 1. As our main focus was to evaluate the (conditional) effects of $\Delta\log[SL]$ on $\Delta\log[B]$, all models had a fixed intercept of 0 for the covariate functions. We conducted all analyses as mixed models (Mixed Procedure in SAS 9.4) with species included as a random effect.

Table 1. Sixty-three cases of changes of hunting seasons and bag size of 28 different game species in Denmark, 1957–2007.

Species	Type ^a	year ^b	reason ^c	Duration of hunting season ^d		Hunting days ^e		Hunting bag change ^f				
				Before	After	before	after	Δlog[SL]	Δlog[B]	SE	DF	Sign.
Red deer <i>Cervus elaphus</i>	NP,S	1967	Ethical	.	.	161	151	-0.03	0.080	0.054	6	
Red deer <i>Cervus elaphus</i>	NP,S	1982	Popul.	.	.	151	143	-0.02	-0.012	0.063	6	
Red deer <i>Cervus elaphus</i>	NP,S	1987	Ethical	.	.	143	133	-0.03	0.059	0.048	6	
Fallow deer <i>Dama dama</i>	NP,S	1967	Ethical	.	.	161	151	-0.03	0.002	0.090	6	
Fallow deer <i>Dama dama</i>	NP,S	1982	Popul.	.	.	151	143	-0.02	0.104	0.053	6	
Fallow deer <i>Dama dama</i>	NP,S	1987	Ethical	.	.	143	133	-0.03	-0.089	0.059	6	
Roe deer <i>Capreolus capreolus</i>	NP,S	1997	Popul.	.	.	112	123	0.04	0.056	0.025	6	
Brown hare <i>Lepus europaeus</i>	NP,S	1994	Other	1 Oct - 18 Dec	1 Oct - 31 Dec	79	92	0.07	0.028	0.039	6	
Brown hare <i>Lepus europaeus</i>	NP,S	2004	Popul.	1 Oct - 31 Dec	1 Oct - 15 Dec	92	76	-0.08	-0.009	0.034	6	
rabbit <i>Oryctolagus cuniculus</i>	NP,S	1990	Ethical	Year round	1 Sep - 31 Jan	365	153	-0.38	-0.039	0.047	6	
Red squirrel <i>Sciurus vulgaris</i>	NP,S	1967	Ethical	Year round	16 Jun - 29 Feb	365	258	-0.15	0.087	0.068	6	
Red squirrel <i>Sciurus vulgaris</i>	NP,S	1982	Ethical	16 Jun - 29 Feb	1 Sep - 29 Feb	258	181	-0.15	-0.105	0.096	6	
Red fox <i>Vulpes vulpes</i>	P,S	1967	Ethical	Year round	16 Jun - 29 Feb	365	258	-0.15	-0.007	0.027	6	
Red fox <i>Vulpes vulpes</i>	P,S	1982	Ethical	16 Jun - 29 Feb	16 Jun - 15 Feb	258	245	-0.02	0.004	0.030	6	
Red fox <i>Vulpes vulpes</i>	P,S	1994	Ethical	16 Jun - 15 Feb	1 Sep - 31 Jan	245	153	-0.20	-0.054	0.036	6	
Badger <i>Meles meles</i>	P,S	1967	Ethical	Year round	16 Jun - 29 Feb	365	258	-0.15	0.081	0.049	6	
Badger <i>Meles meles</i>	P,S	1982	Ethical	16 Jun - 29 Feb	16 Jun - 15 Feb	258	245	-0.02	-0.007	0.076	6	
Badger <i>Meles meles</i>	P,S	1990	Ethical	16 Jun - 15 Feb	1 Oct - 15 Feb	245	138	-0.25	0.037	0.081	4	
Stone marten <i>Martes foina</i>	P,S	1967	Ethical	Year round	16 Jun - 29 Feb	365	258	-0.15	0.070	0.038	6	
Stone marten <i>Martes foina</i>	P,S	1982	Ethical	16 Jun - 29 Feb	16 Jun - 15 Feb	258	245	-0.02	0.048	0.040	6	
Stone marten <i>Martes foina</i>	P,S	1994	Ethical	16 Jun - 15 Feb	1 Sep - 31 Jan	245	153	-0.20	0.040	0.053	6	
Grey partridge <i>Perdix perdix</i>	NP,S	1967	Other	18 Sep - 1 Nov	16 Sep - 31 Oct	45	46	0.01	-0.106	0.025	6	**
Grey partridge <i>Perdix perdix</i>	NP,S	1994	Other	16 Sep - 31 Oct	16 Sep - 30 Nov	46	76	0.22	0.018	0.049	6	
Grey partridge <i>Perdix perdix</i>	NP,S	2004	Popul.	16 Sep - 30 Nov	16 Sep - 31 Oct	76	46	-0.22	0.096	0.085	6	
Pheasant <i>Phasianus colchicus</i>	NP,S	1958	Popul.	.	.	92	67	-0.14	-0.095	0.092	6	
Pheasant <i>Phasianus colchicus</i>	NP,S	1990	Popul.	.	.	67	74	0.05	0.003	0.061	6	
Pheasant <i>Phasianus colchicus</i>	NP,S	1994	Popul.	.	.	74	90	0.08	0.030	0.041	5	
Wood pigeon <i>Columba palumbus</i>	NP,S	1994	Ethical	1 Aug - 31 Dec	1 Sep - 31 Dec	153	153	0.00	0.094	0.039	6	
Wood pigeon <i>Columba palumbus</i>	NP,S	2007	Ethical	1 Sep - 31 Dec	1 Oct - 31 Dec	153	123	-0.09	0.277	0.095	5	*
Collared dove <i>Streptopelia decaocto</i>	NP,S	1979	Popul.	1 Nov - 30 Nov	1 Oct - 30 Nov	30	61	0.31	0.206	0.091	6	
Collared dove <i>Streptopelia decaocto</i>	NP,S	1994	Popul.	1 Oct - 30 Nov	1 Oct - 31 Dec	61	92	0.18	-0.008	0.053	6	
Collared dove <i>Streptopelia decaocto</i>	NP,S	2004	Popul.	1 Oct - 31 Dec	1 Oct - 30 Nov	92	61	-0.18	-0.078	0.075	4	
Collared dove <i>Streptopelia decaocto</i>	NP,S	2007	Ethical	1 Oct - 30 Nov	1 Nov - 31 Dec	61	61	0.00	-0.001	0.121	3	
Greylag goose <i>Anser anser</i>	NP,NS	1994	Ethical	1 Aug - 31 Dec	1 Sep - 31 Dec	153	122	-0.10	-0.015	0.034	5	
Mallard <i>Anas platyrhynchos</i>	NP,S	1957	Ethical	1 Aug - 31 Dec	15 Aug - 31 Dec	153	139	-0.04	0.019	0.112	6	
Mallard <i>Anas platyrhynchos</i>	NP,S	1967	Other	15 Aug - 31 Dec	16 Aug - 31 Dec	139	138	0.00	-0.063	0.026	6	
Mallard <i>Anas platyrhynchos</i>	NP,S	1982	Ethical	16 Aug - 31 Dec	1 Sep - 31 Dec	138	122	-0.05	0.041	0.028	6	
Common teal <i>Anas crecca</i>	NP,NS	1982	Ethical	16 Aug - 31 Dec	1 Sep - 31 Dec	138	122	-0.05	-0.024	0.054	6	
Wigeon <i>Anas penelope</i>	NP,NS	1982	Ethical	16 Aug - 31 Dec	1 Sep - 31 Dec	138	122	-0.05	-0.024	0.054	6	
Eider <i>Somateria mollissima</i>	NP,NS	1954	Ethical	1 Sep - 29 Feb	1 Sep - 31 Dec	181	153	-0.07	-0.219	0.415	4	
Eider <i>Somateria mollissima</i>	NP,NS	1957	Ethical	1 Sep - 31 Jan	1 Oct - 29 Feb	153	151	-0.01	-0.223	0.095	4	

Continued

Table 1. Continued.

Species	Type ^a	year ^b	reason ^c	Duration of hunting season ^d		Hunting days ^e		Hunting bag change ^f			Sign.
				Before	After	before	after	$\Delta\log[B]$	SE	DF	
Eider <i>Somateria mollissima</i>	NP,NS	1994	Popul.	1 Oct - 29 Feb	1 Oct - 31 Jan	151	123	-0.015	0.087	6	
Eider <i>Somateria mollissima</i>	NP,NS	2004	Popul			123	115	0.009	0.036	6	
Common scoter <i>Melanitta nigra</i>	NP,NS	1967	Other	1 Sep - 29 Feb	1 Oct - 29 Feb	181	151	-0.026	0.045	3	
Common scoter <i>Melanitta nigra</i>	NP,NS	1994	Other	1 Oct - 29 Feb	1 Oct - 31 Jan	151	123	-0.09	0.119	6	
Common pochard <i>Aythya ferina</i>	NP,NS	1967	Other	15 Aug - 31 Jan	16 Aug - 29 Feb	170	197	0.06	0.024	3	**
Common pochard <i>Aythya ferina</i>	NP,NS	1982	Other	16 Aug - 29 Feb	1 Sep - 29 Feb	197	181	-0.04	0.149	6	
Common pochard <i>Aythya ferina</i>	NP,NS	1994	Other	1 Sep - 29 Feb	1 Oct - 31 Jan	181	123	-0.17	0.200	6	
Red breasted merganser <i>Mergus serrator</i>	NP,NS	1994	Other	1 Oct - 29 Feb	1 Oct - 31 Jan	151	123	-0.09	0.178	5	
Herring gull <i>Larus argentatus</i>	P,NS	1987	Other	16 Aug - 30 Apr	1 Sep - 29 Feb	258	181	-0.15	0.145	3	
Herring gull <i>Larus argentatus</i>	P,NS	1994	Other	1 Sep - 29 Feb	1 Sep - 31 Jan	181	153	-0.07	0.063	6	
Great black-backed gull <i>Larus marinus</i>	P,NS	1987	Other	16 Aug - 30 Apr	1 Sep - 29 Feb	258	181	-0.15	0.164	3	
Great black-backed gull <i>Larus marinus</i>	P,NS	1994	Other	1 Sep - 29 Feb	1 Sep - 31 Jan	181	153	-0.07	0.101	6	
Common coot <i>Fulica atra</i>	NP,NS	1982	Other	16 Aug - 29 Feb	1 Sep - 29 Feb	197	181	-0.04	0.130	6	
Common coot <i>Fulica atra</i>	NP,NS	1994	Other	1 Sep - 29 Feb	1 Sep - 31 Jan	181	153	-0.07	0.079	6	
Eurasian woodcock <i>Scolopax rusticola</i> ^h	NP,NS	1967	Ethical	1 Jan - 7 Apr	1 Mar - 7 Apr	98	38	-0.41	0.151	6	
Eurasian woodcock <i>Scolopax rusticola</i>	NP,NS	1973	Ethical			137	99	-0.14	0.092	6	
Eurasian woodcock <i>Scolopax rusticola</i>	NP,NS	1982	Other	24 Sep - 31 Dec	1 Oct - 31 Dec	99	92	-0.03	0.076	6	
Eurasian woodcock <i>Scolopax rusticola</i>	NP,NS	2004	Popul.	1 Oct - 31 Dec	1 Oct - 15 Jan	92	107	0.07	0.118	6	
Snipes ^h	NP,NS	1967	Other	15 Aug - 31 Dec	16 Aug - 31 Dec	139	138	0.00	0.038	6	
Snipes ^h	NP,NS	1982	Other	16 Aug - 31 Dec	1 Sep - 31 Dec	138	122	-0.05	0.033	6	
Hooded crow <i>Corvus corone</i>	P,S	1967	Ethical	Year round	1 Jul - 30 Apr	365	304	-0.08	0.031	6	
Common magpie <i>Pica pica</i>	P,S	1967	Ethical	Year round	1 Jul - 30 Apr	365	304	-0.08	0.016	6	

^aGame categories (P: predator, NP: non-predator, S: sedentary in the hunting season, NS: non-sedentary in the hunting season)

^bThe year the hunting season was changed

^cReason for changing the hunting seasons (Popul.: population considerations, Ethical: ethical reasons, Other: other reasons)

^dThe duration of the hunting seasons are not shown for species with differentiated hunting seasons for different population segments (e.g. males and females: in such cases hunting season lengths were averaged over the segments)

^e $\Delta\log[SL] = \log_{10}(\text{number of hunting days after/before the change of hunting season})$

^fThe raw data (entire Danish game statistics 1941–2009) are publicly available at [http://dce.au.dk/fileadmin/Resources/DMU/Dyr%20og%20-%20%20log\[B\] = \log_{10}\(\text{bag size after/before the change of hunting season}\)](http://dce.au.dk/fileadmin/Resources/DMU/Dyr%20og%20-%20%20log[B] = \log_{10}(\text{bag size after/before the change of hunting season})). DFD = number of years with bag statistics up to 5 years on each side of the change in hunting season (i.e. maximum 10) - 4 (estimation of intercept, $\Delta\log[B]$ and longitudinal trends in $\log[B]$ before and after the change of the season) = maximum 6 (A lower number of df is due to fewer years with bag data before and after the change of hunting seasons). Sign.: *: $p < 0.05$, **: $p < 0.01$

^gSeparate statistics for the spring hunting season

^hCommon snipe *Callinago gallinago* and Jack snipe *Lymnocyrtes minimus*

To test whether the functional relationship between $\Delta\log[B]$ and $\Delta\log[SL]$ was conditional on: game species, reasons for introducing the change in hunting season, or interacted with changes in median date of the season or the span of years over which hunting season changes had been recorded, we evaluated a set of candidate models including these differential responses on the basis of the AICc-criterion.

We categorized the different species types as either predominantly sedentary ($n = 38$) or non-sedentary ($n = 25$) during the hunting season. As non-sedentary game species are more likely to be replaced if locally depleted in numbers, we hypothesised that hunters would be less motivated to limit their harvest effort on non-sedentary compared to sedentary game species. Many of these non-sedentary species are hunted on sea territories where hunters are not confined to hunt within a hunting area of limited size and may not feel compelled to spare the stock (following the exploitation of the commons principle: Hardin 1968). In that case, harvest size should correlate more strongly with the length of the season in non-sedentary species than in sedentary species. As a result, the slope of the $\Delta\log[B] - \Delta\log[SL]$ function should be steeper and closer to 1 in non-sedentary compared to sedentary species.

We also categorized game species as either predatory ($n = 15$) or non-predatory ($n = 48$). If predatory species were killed as an effort to control their populations, the $\Delta\log[B] - \Delta\log[SL]$ response could either be stronger (assuming hunters used every chance available within the open season to kill off predators) or weaker (assuming hunters aimed to kill a pre-defined number of predators or to depress their numbers below a given threshold) than for non-predatory game species.

We categorized the primary reasons for changing the hunting season as 'population management' (to decrease hunting pressure on a species to favour population growth rate or to release hunting restriction on a species considered to be able to sustain a higher harvest: $n = 14$), 'ethical considerations' (typically reduction of the hunting seasons to avoid periods of the year when breeding activities take place: $n = 30$), and 'other reasons' (mainly harmonization of hunting seasons across several species with different seasons to simplify rules, $n = 19$). A priori, we expected the strongest effect of $\Delta\log[SL]$ on $\Delta\log[B]$ in cases where the change in season length were motivated by population management aims, as these season changes should be those most directed towards a change in harvest size. We expected the least effect when seasons were changed because of ethical concerns, as many hunters for the same ethical reasons voluntarily might have refrained from hunting in those periods that were closed to them later.

We used the difference in median dates (number of days counted from the start of the year when the season started) between the initial and second hunting season as a measure for an effect of whether the season was advanced or delayed. Hence, if a season was shortened by one month in the end the median date of the season decreased by 15 days. As population sizes and thereby also the harvestable stock in many species, because of other natural causes, may decrease with advancing dates increasing median dates could have a negative impact on $\Delta\log[B]$ as a simple main effect as well as in interaction with $\Delta\log[SL]$.

Assuming hunters invest a fixed, maximum effort or desire a specific yield within a given season, the effect of a relative reduction in season length on $\Delta\log[B]$ may be more severe if the initial season is short than if it is long because the hunters then may be more likely to become constrained in their hunting effort. For the same reason, we tested whether the effect of relative season length interacted with its absolute length before being changed.

We used the year of hunting season change (1957–2007) as a covariate for analyses of possible changes in hunter response to changes in hunting seasons.

We ranked candidate models representing the aforementioned hypotheses on the basis of AICc-weights, and compared them with a 'base' model with no fixed effects. Because models including interactions between $\Delta\log[SL]$ and reasons for changing hunting season and models with interactive effects of whether the species was sedentary or non-sedentary had higher support in the data than other models, we also evaluated models with the combined effects of these two factors.

All models included heteroscedasticity (variance heterogeneity) between sedentary and non-sedentary species, as these models had consistently lower AICc-values than models without differential variance functions ($\Delta AICc = 5-8$). However, fixed effect predictions were relatively similar for models with and without heteroscedasticity, as were the relative $\Delta AICc$ -values of the different fixed-effect models.

Results

In the 63 cases of hunting season length changes (Table 1), initial season lengths ranged from 30 to 365 days (median = 153), and the changed season lengths varied from 39 to 204 % of the initial lengths (median = 88 %). The subsequent hunting season lengths varied from 38 to 304 days (median = 138).

Three out of 63 changes of hunting seasons were followed by significant changes in the annual bag size (Table 1). However, the number of statistically significant results were no greater than that expected by chance from the total number of test cases (the nil expectation was 3.15 type 1 errors from 63 tests with $\alpha = 5\%$), and two of the statistically 'significant' changes represented trends in the opposite direction to the initial predictions of a positive correlation between and $\Delta\log[B]$ and $\Delta\log[SL]$.

The top-ranked model (Akaike's weight = 95%) predicted differential slopes between $\Delta\log[B]$ and $\Delta\log[SL]$ for sedentary and non-sedentary species in interaction with motives for changing the seasons (Table 2). Models predicting differential slopes for either residency status or reasons for changing the seasons, performed modestly better than the base model predicting no effects (evidence ratios of Akaike's weights = 4.1–4.5, Table 2). A model predicting the same response in $\Delta\log[B]$ as a function of $\Delta\log[SL]$ across all cases had about the same support as the 'no effect' model (evidence ratio = 0.8, Table 2), as had a model that discriminated between predatory and non-predatory species (evidence ratio = 0.7, Table 2). Models taking change of median season date, initial length of the hunting season and

Table 2. Differences in Akaike's information criterion corrected for sample size ($\Delta AICc$) ranking and Akaike's weights (w_i) of mixed models for variation in relative change in the Danish national bag size as function of relative changes in the length of the hunting season ($\Delta \log[SL]$). R: reason for the change in hunting season (population management, ethical concerns or other reasons); S/NS: whether a species was sedentary or non-sedentary (migratory or nomadic) in the hunting season; P: whether a species was predatory or non-predatory in relation to game interests; L: initial hunting season length; ΔMD : Change in median date of hunting season. K: number of fixed effect parameters. ER: evidence ratio (ratio of $AICc$ weights) relative to model with no fixed effects. All models had species included as random effect and different variances specified for S/NS.

Fixed effects model	K	$\Delta AICc$	w_i	ER to 'no effects'
$\Delta \log[SL] \times S/NS \times R$	6	0.0	0.95	424
$\Delta \log[SL] \times S/NS \times \Delta \log[SL] \times R$	5	7.3	0.02	11
$\Delta \log[SL] \times S/NS$	2	9.1	0.01	4.5
$\Delta \log[SL] \times R$	2	9.3	0.01	4.1
(no effects)	0	12.1	0.00	–
$\Delta \log[SL]$	1	12.5	0.00	0.8
$\Delta \log[SL] \times P$	2	12.7	0.00	0.7
ΔMD	1	24.4	0.00	0.002
$\Delta \log[SL] \times L$	1	25.4	0.00	0.001
$\Delta \log[SL] \times \text{year}$	1	27.7	0.00	0.0004
$\Delta MD + \Delta \log[SL] \times \Delta MD$	2	32.7	0.00	0.00003

year into account, all performed considerably worse than the 'no effect' model (evidence ratios ≤ 0.002 , Table 2).

The estimated slopes from the top-ranked model suggested the strongest response in $\Delta \log[B]$ as function of $\Delta \log[SL]$ in non-sedentary species when seasons were changed because of 'other' reasons, as the slope was close to

1 and significantly above 0 ($p = 0.0057$), indicating that $\Delta \log[B]$ on average was proportional with $\Delta \log[SL]$ for this category (Table 3). An effect of $\Delta \log[SL]$ on $\Delta \log[B]$ also tended to exist in season lengths changed for 'ethical reasons' in non-sedentary species (slope = 0.49, $p = 0.054$), whereas no functional relation appeared to exist for the other four category combinations (Table 3). The (lower ranked) model that only differentiated slopes between sedentary and non-sedentary species, suggested a functional relationship between $\Delta \log[SL]$ and $\Delta \log[B]$ in non-sedentary species only (slope = 0.54, Table 3). The (similarly ranked) model that only differentiated between reasons for changing the seasons, suggested an effect in cases where the season had been changed because of 'other' reasons (slope = 0.62, Table 3). The (even lower ranked) model that estimated $\Delta \log[B]$ on $\Delta \log[SL]$ across all cases, suggested a non-significant effect of $\Delta \log[SL]$ on $\Delta \log[B]$ (slope = 0.16, $p = 0.12$, Table 3).

All aforementioned functional relations between $\Delta \log[B]$ and $\Delta \log[SL]$ were estimated with considerable uncertainty. Hence, the 95% confidence interval for the estimated mean change in bag size upon a 50% season length reduction for all cases pooled, ranged from 78 to 103 % (mean = 90%) of the initial bag size (Table 3, Fig. 1a). In other words: halving the hunting season length would in general (all cases pooled) result in an estimated 10% decrease in mean bag size with a 95% confidence interval ranging from a 22% decrease to a 3% increase. The uncertainty for the same estimate for non-sedentary species and a season change due to 'other reasons' (the case group with the strongest and statistically most significant relation between $\Delta \log[B]$ and $\Delta \log[SL]$: Table 3) ranged from 30 to

Table 3. Relative change in Danish national bag size as functions of relative changes in the length of the hunting season, divided on reasons for changing the hunting season lengths and species types (non-sedentary or sedentary). The predictions are based on the mixed models presented in Table 2 (same notation). Statistical significances are given for t -tests of whether the slopes (B) are different from 0 (change in bag size not related to change in hunting season length) or 1 (change in bag size proportional with change in hunting season length). LCL and UCL: lower and upper 95% confidence limits of the mean.

Model	Case categories		Slope					Hypotheses ^a		Relative bag size at 50% season length reduction ^b		
	Reason	Species type	B	SE	DF	LCL	UCL	$P_{(B=0)}$	$P_{(B=1)}$	mean	LCL	UCL
$\Delta \log[SL]$.	.	0.16	0.10	34	-0.04	0.36		****	0.90	0.78	1.03
$\Delta \log[SL] \times S/NS$.	non-sedentary	0.54	0.20	33	0.14	0.95	**	*	0.69	0.52	0.91
		sedentary	0.05	0.11	33	-0.18	0.27		****	0.97	0.83	1.13
$\Delta \log[SL] \times R$	other	.	0.62	0.27	32	0.07	1.18	*		0.65	0.44	0.95
	ethical	.	0.03	0.13	32	-0.22	0.29		****	0.98	0.82	1.17
	population	.	0.25	0.19	32	-0.13	0.63		***	0.84	0.64	1.10
$\Delta \log[SL] \times S/NS \times R$	other	non-sedentary	1.04	0.35	29	0.33	1.75	**		0.49	0.30	0.80
	other	sedentary	0.09	0.39	29	-0.71	0.90		*	0.94	0.54	1.64
	ethical	non-sedentary	0.49	0.24	29	-0.01	0.99	(*)	*	0.71	0.50	1.01
	ethical	sedentary	-0.10	0.14	29	-0.38	0.18		****	1.07	0.88	1.30
	population	non-sedentary	-1.15	0.94	29	-3.07	0.76		*	2.22	0.59	8.39
	population	sedentary	0.29	0.18	29	-0.08	0.67		***	0.82	0.63	1.06

^aStatistical significances of tests of slopes (B) being 0 (no relation between change in season length and bag size) and 1 (change in bag size being proportional to change in season length); (*): $p < 0.10$ (one-tailed: $p < 0.05$), **: $p < 0.05$, ***: $p < 0.01$, ****: $p < 0.001$, *****: $p < 0.0001$)

^bPredicted bag size if the season length is halved (1.00 = same bag size as before a reduction [no difference], 0.50 = bag size halved if season length is halved [change in bag size proportional with change in season length])

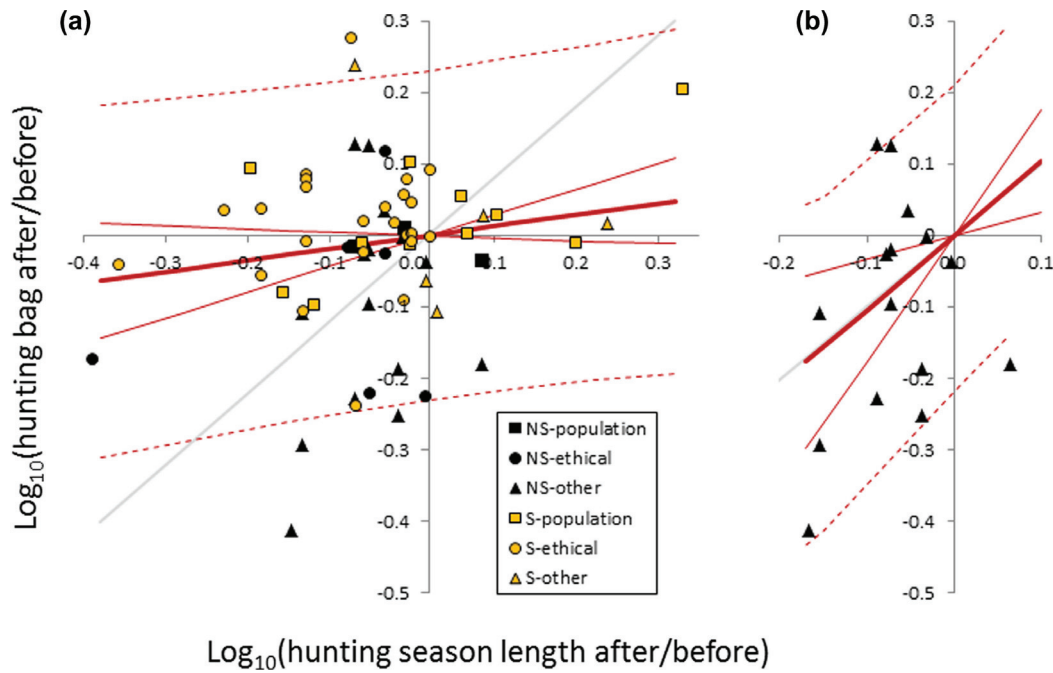


Figure 1. (a) Relative changes in the Danish national hunting bag plotted against relative change in hunting season length in 63 cases of changes of nationwide hunting seasons. Different symbols represent different species type (sedentary [S] or non-sedentary [NS] species during the hunting season) and reasons for changing hunting season lengths. In (b) is shown a subset consisting of 15 cases of non-sedentary species with the hunting season changed for 'other' reasons. In both graphs, thick, full lines indicate regression lines from mixed models (see Table 3 for equations), thin, full lines 95% confidence zones for the regression line, and thin, punctuated lines 95% confidence zones of the individual observations. The thin, full, grey line ($y = x$) indicates the predicted relationship if changes in hunting season length are proportional with changes in bag size.

80% (mean = 49%) of the initial bag size (Table 3, Fig. 1b). In all cases, confidence limits for point estimates were so broad that no reasonable predictions could be made about the anticipated effects of a given change in relative season length on harvest size within the observation range (Fig. 1a–b).

Discussion

The bag data analysed here covers a variety of species hunted using different methods, in different landscape types and by different segments of the Danish hunter population. The geographical scale and the number of hunters involved is so large (entire Denmark and > 100 000 active hunters reporting bag statistics annually) that the focus of the analyses presented here are the emergent patterns of regulatory changes rather than capturing the specific, behavioural mechanisms that may make hunters kill more or less game as a result of national hunting season regulations. It is also important to stress that only 14 out of the 63 hunting season changes were explicitly motivated by population management aims. For the same reason, our aim is not to provide an accurate predictive analysis of how large an effect on bag size one should expect for a given change in hunting season length, but to analyse the extent to which changes in season length affects bag size in general. Because our method of estimating the relative change in national bag size ($\Delta\log[B]$) eliminates effects of longitudinal trends in the national bag size, which could be due to

changes in population size or number of active hunters, $\Delta\log[B]$ should be reasonable index for the immediate change in harvest rate (proportion of individuals harvested). We would also stress that although we failed to find consistent effects of changes in the median date of the hunting seasons, we acknowledge that for certain game species the seasonal timing of hunting seasons may have profound effects on the harvest either because of natural mortality (Palmer and Bennett 1963, Brøseth et al. 2012), or because of seasonality in exposure and vulnerability to hunters (Merkel 2010).

We found support for higher sensitivity in $\Delta\log[B]$ to $\Delta\log[SL]$ in non-sedentary than in sedentary species in interaction with the motivation for changing the season: the strongest effect of $\Delta\log[SL]$ on $\Delta\log[B]$ was found in seasons changed for 'other' reasons in non-sedentary species, where $\Delta\log[B]$ varied in proportion non-sedentary species, where $\Delta\log[B]$ varied in proportion with $\Delta\log[SL]$ (slope = 1). An intermediate response appeared when hunting seasons were changed for 'ethical' reasons in non-sedentary species ($0 < \text{slope} < 1$), whereas no significant correlations could be established between $\Delta\log[SL]$ and $\Delta\log[B]$ in sedentary species and/or in cases where the season lengths were changed for population management objectives. Hence, apparently, Danish hunters changed their total harvest of non-sedentary species proportional with the change of the season length when the reason for the change was a general harmonization of hunting season dates across species, partially if the season was changed for 'ethical' reasons, and maintained a constant, total harvest in all other cases. Hence, for sedentary species and in cases

where the length of a hunting season was changed to achieve a higher or lower harvest rate, hunters seemed to compensate for varying lengths of the hunting season by adjusting their effort within the time available. The overall pattern of weak influence of changes in hunting season lengths on bag size fits well with the general notion expressed long ago (Joensen 1974, p. 171) that most Danish sea bird hunters aim for a fixed number of hunting trips and/or killed game per hunting season, regardless of its length.

A generally stronger response in $\Delta\log[B]$ in relation to $\Delta\log[SL]$ for non-sedentary than for sedentary species was in accordance with our predictions, because sedentary game species are primarily hunted on private grounds where local hunting pressure is typically adjusted in accordance with local population management aims according to hunters' own assessment of local abundance (Primdahl et al. 2012). Non-sedentary species on private estates as well as sea ducks may, to a larger extent, be considered as a renewable resource harvested in competition with other hunters. Here there may be fewer incentives for individual hunter's to adjust the size of their harvest out of concern for the local game stock (Hardin 1968). However, even for non-sedentary species, the regression slope was lower than 1, suggesting other reasons explain the more constant yield than would be expected from the variation in season length per se if hunter satiation was motivated by population concerns. In an analysis of variation in the national Danish bag size of common eiders *Somateria mollissima* (that are hunted from small boats on the sea), Christensen (2005) found that the annual harvest per active hunter was constant across years despite considerable annual variation in the number of days with suitable weather conditions and in size and demographic composition of the population. We imagine that a similar allocation of effort (i.e. where hunters aim at a pre-determined cumulative effort or yield over the season) may be widespread amongst recreational hunters even when they share hunting areas with others (Willebrand et al. 2011).

As an exception to the overall picture of no or weak effects of $\Delta\log[SL]$ on $\Delta\log[B]$, bag sizes changed in proportion with the changes of the season lengths when these were changed for 'other' reasons in non-sedentary species. In practice, 'other' reasons for changing the season lengths were typically harmonisations in the durations of hunting seasons across different species to simplify hunting season rules. Such harmonisations of seasons results in greater overlap of hunting periods between related species (e.g. sea ducks), possibly having a 'dilution effect' on the hunting effort for all individual species as more species were concurrently available in the revised hunting seasons. As a result, hunting pressures on the individual species may have decreased.

To our surprise, the $\Delta\log[B] - \Delta\log[SL]$ relations were not significantly different from 0 for cases where season lengths were changed to promote a change in harvest size. One can only speculate about this lack of response in bag size where a response was intended. The result indicates that changes in nationwide hunting season lengths of the type reported in these results do not offer an efficient harvest management tool to reduce or increase the size of hunting bags. The weak relationships between mean changes in bag

size and season length and the considerable scatter around statistically significant functions supports the notion, held by many wildlife managers (Pellikka et al. 2005), that reducing or expanding the general hunting season does not appear to be an effective harvest management tool for populations with hunting seasons lasting for a month or more.

All of the examples of positive correlations between changes in the harvest season for recreational hunters on bag size, harvest rate, total mortality rate or even population growth rates of which we are aware had seasons lasting less than 30 days (often less than 10 days: Skurdal et al. 1997, Heusmann and McDonald 2002, Norman et al. 2004, Fleskes et al. 2007, Dooley et al. 2010, Chamberlain et al. 2012) or resulted from a total hunting ban (Geis and Crissey 1969). We therefore conclude that if no detailed prior information exists about the harvest effort and total yield as a function of season length of recreational hunters in a given system, national managers should not expect any measurable regulating effects of hunting season length on total harvest yield, at least as long the season exceeds one month. This general result does not exclude the possibility that regulation of the length of the open hunting season can be used as the only harvest regulation tool in an adaptive harvest management strategy, but in that case, the 'functional response' of hunters in relation to the length and timing of the hunting season should be known in advance in order to anticipate the harvest and population effects with any reasonable precision. However, this will require a far more detailed insight into the hunters' motives and behavioural decisions behind their engagement in hunting activities and the extent to which they kill game than is presently available e.g. for Danish hunters. Finally, we would also stress that the present patterns may only apply to recreational hunters who only devote a limited amount of their potentially available time leisure to hunting activities. In systems where natural resources are harvested for subsistence or income (e.g. by indigenous people in the Arctic, Merkel 2010), exploitation effort may well correlate more closely with season length than appear to be the case in this example.

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