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Using human-dimensions research to reduce implementation uncertainty for wildlife management: a case of moose (*Alces alces*) hunting in northern Ontario, Canada

Len M. Hunt

Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada. Email: len.hunt@ontario.ca

Abstract

Context. Wildlife managers frequently use regulations to alter the preferred hunting strategies and outcomes of hunters. However, hunters can respond to changing social and resource conditions resulting from regulations in ways that can surprise wildlife managers.

Aims. The specific research questions were (1) how does the availability of licences (tags) required to harvest adult moose (*Alces alces*) relate to the success of hunters at filling these tags and (2) how do hunting pressure and the density of calf moose relate to the harvest rate of the calf population.

Methods. Information about hunters, harvest-related outcomes and moose abundance were estimated from social surveys and aerial inventories in 46 wildlife management units (WMUs) in northern Ontario, Canada. An information-theoretic approach was used to select regression models that predicted the average annual filling rate of tags for adult moose and for the average annual proportion of calf population harvested by hunters in the WMUs.

Key results. Tag filling rates were negatively and strongly associated with the availability of tags to hunters in the WMUs. The proportion of calf population harvested was positively related to hunting pressure and negatively related to the density of calf populations in the WMUs.

Conclusions. As tags became more scarce, hunters appeared to become more skilled at harvesting adult moose. As calf density declined, hunters harvested larger proportions of the population, indicating a possible inverse density-dependent relationship between abundance and harvest.

Implications. Understanding hunters and their actions and role within a larger social-ecological system are critical for helping to reduce the uncertainty of implementing regulations for managing wildlife. Without having this understanding, it is easy for managers to become trapped in situations where the intent of management actions is undermined by the abilities of hunters who respond to both changing social and resource conditions.

Additional keywords: behaviour, econometrics.

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Introduction

It is almost a cliché to state that managing wildlife is really about managing people's expectations and actions. Wildlife species are managed primarily because human actions such as hunting or industrial development directly or indirectly affect animal behaviours, recruitment, morbidity and/or mortality. The effects of human actions on wildlife are probably most apparent for hunting. Hunting results in many undesirable effects on wildlife, wildlife populations and ecosystem function (e.g. Fa and Brown 2009). Consequently, people design institutions (i.e. rules, norms or shared strategies, Crawford and Ostrom 2005) to encourage or discourage actions by people such as hunting regulations.

In Canada and the United States, the constitutive institutional design assigns wildlife management rights and responsibilities to government agencies (Jacobson and Decker 2006). In turn, these agencies construct roles and responsibilities for different actors (e.g. identify who are hunters), design decision-making processes, develop rule-based (regulation-based) institutions and conduct enforcement activities. Rules are developed to help achieve goals such as biological sustainability of wildlife populations, safety, fairness of hunting benefits, and fair chase that result in restrictions and prohibitions on hunting or certain hunting strategies. The rules can affect the number of hunters, their harvests, and/or the seasons, times, locations, gear and equipment and target species (including age and sex) that constitute a legal hunting strategy. The hope is to find a careful balance where people are encouraged to enjoy hunting and the harvesting of game, while limiting harvests to levels that can sustain wildlife populations.

Unregulated hunting exploitation is especially a concern for long-lived and large-bodied mammals with slow reproduction rates (Peres 2000). Consequently, regulations that seek to limit the number of hunters or harvested animals, such as the selective harvest system, are frequently used for big-game management (e.g. Fulton and Hundertmark 2004; Giles and Findlay 2004). This system allows managers to control and distribute a limited number of licences (tags) required to hunt certain wildlife species, including the sex and age of animals. Hunters have largely accepted these controls on their hunting actions (e.g. Fulton and Hundertmark 2004).

A good understanding of wildlife populations and wildlife harvest by hunters is a key for actively managing wildlife populations, especially with a selective harvest system. Whereas estimating wildlife populations is a complex and challenging subject (see Boyce *et al*. 2012, for pragmatic considerations), the focus here is on wildlife harvest by hunters. Estimating wildlife harvest often proceeds without careful attention to understand the hunter and his/her actions (Stedman *et al*. 2004). However, people alter their hunting strategies as resource and social conditions change (e.g. Vaske *et al*. 2004; Alves *et al*. 2009) and may increasingly value and target scarce species (Palazy *et al*. 2012). This behavioural plasticity, along with differences in hunting skill, can greatly affect hunters' abilities to exploit resources (e.g. Bowyer *et al*. 1999; Schmidt *et al*. 2005). It is contended here that the adaptability of hunters heightens concerns about implementation uncertainty (Bunnefeld *et al*. 2011) when managing wildlife through regulations. Without carefully understanding the hunter and, thus, reducing implementation uncertainty, managers can be trapped in situations where attempts to regulate wildlife harvest can result in surprising responses by hunters who change their actions to maintain wildlife harvests.

This contention is examined for the case of moose hunting in northern Ontario, Canada. The Ontario Ministry of Natural Resources (OMNR) uses a selective harvest system for bull and cow moose, with specific allocations of tags by WMU for tourist operators, resident gun hunters and resident archers (OMNR 2012). In northern Ontario, calf-moose hunting is open to any eligible person who purchases a moose-hunting licence. Using moose population, moose harvest, hunter and other data at the WMU scale in northern Ontario, Canada, the following research questions were examined:

(1) how does the availability of licences (tags) for bull and cow moose in WMUs relate to the success rate of hunters at filling these tags; and
(2) how do hunting pressure and the relative abundance of calf populations within a WMU relate to the harvest rate of the calf population?

The first question focuses on understanding the responses by hunters to varying social (managerial) conditions. Economic theory suggests that as available tags become scarce, they become more valuable to hunters. Therefore, it is expected that hunters will respond to this scarcity by finding ways to increase their ability to fill a tag.

The second question focuses on responses by hunters to varying resource conditions. Given that calf-moose hunting in northern Ontario is open to all licenced moose hunters, it is necessary to account for changing levels of hunting pressure (i.e. a density measure of days hunted for moose in a WMU) on calf harvesting, before assessing relationships between calf-moose density and calf harvest rates. The harvest rate of the calf population should increase with hunting pressure (i.e. more hunting leads to larger relative effects). However, it is an empirical question whether the calf harvest rate is associated with the calf-moose density. If a negative relationship exists, it implies that hunters harvest a larger share of the calf population as calf density declines. In other words, the skill of hunters offsets some effects of declining wildlife abundance on hunters' abilities to harvest calf moose. Other researchers have noted potential density-dependent harvests by moose hunters (e.g. Bowyer *et al*. 1999; Hatter 2001).

More than the availability of tags affects the abilities of hunters to fill tags for bull and cow moose. Moose density should also influence harvest success. From the general result that hunting success increases with wildlife density, it is believed that moose density should be positively related to tag-filling rates, *ceteris paribus*. The accessibility of the WMU to hunters should also influence the abilities of hunters to fill tags. Accessibility is often measured by roads, road density and/or, inversely, as hunters' travel costs or distances (e.g. Haener *et al*. 2001; Stedman *et al*. 2004; Brown 2011). It is believed that as accessibility increases, hunters respond with increased hunting pressure (e.g. Rempel *et al*. 1997; Stedman *et al*. 2004) and harvest success (e.g. Schmidt *et al*. 2005; Shanley and Pyare 2011).

Materials and methods

The research questions were assessed with an information-theoretic approach for model selection (Burnham and Anderson 2010). The information-theoretic approach casts away single null-hypothesis testing in favour of an assessment of evidence for competing models (hypotheses), given a set of models and data (Burnham and Anderson 2010). The approach relies on the relationship between the likelihood statistic and Kullback–Leibler information (Burnham and Anderson 2010).

The Akaike information criterion (AIC) is the key statistic that links Kullback–Leibler information and the likelihood statistic. The model with the lowest AIC has greatest evidence of support, given the data and set of competing models. Following the advice of Burnham and Anderson (2010), the finite sample size-corrected AIC (i.e. AICc) was reported for each model, along with the difference in AICc from the model with a minimum AICc, the Akaike weights (i.e. the exponent of the difference in AICc divided in half) and probability of evidence (i.e. the Akaike weight divided by the sum of all Akaike weights). A summary statistic representing the fit for each model was also provided.

The study area is WMUs in northern Ontario, Canada (Fig. 1). Some WMUs in northern Ontario were excluded from the analysis because they have no moose hunt, information about moose and/or moose hunters was absent or deficient and/or they had very low road densities, resulting in a significantly different type of hunting experience. The WMUs 01A, 01B, 01C, 01D in

Fig. 1. Wildlife management units (WMUs) in Ontario, Canada, and those WMUs included in the study area.

the far north of the province were excluded because of their location away from resident hunters and the absence of roads. Other removed WMUs included 7B and 20 (islands on very large inland lakes), 11C (Quetico Provincial Park where hunting is prohibited), 10 (no available information on hunter harvest success), and 14 (a peninsula and some islands on Lake Superior with a very low road density). The remaining 46 WMUs represented 99.4% of projected moose-hunting days in northern Ontario and 87.3% of projected moose-hunting days in Ontario from 1999 to 2010 (calculated from data described below). Southern Ontario WMUs were excluded because moose-hunting seasons are often much shorter (as little as 1 week, compared with an approximate 10-week season for most northern Ontario WMUs) and some WMUs have a selective harvest system for calves.

Some regulatory differences in moose hunting exist among the 46 WMUs for the present analysis (OMNR 2012). The WMUs in the northern areas often have an earlier start to the gun-hunting season for moose than do those elsewhere (e.g. 15 September, compared with the second Saturday in October). Some of the north-eastern WMUs also have a shorter season length than elsewhere, such as a closure on 15 November rather than 15 December. These rules are designed to encourage hunting and harvest in northern WMUs and reduce harvest in heavily used WMUs in the north-east. Consequently, these rules should reduce hunters' opportunities to harvest moose in areas where tags are scarce (i.e. heavily hunted WMUs).

The dependent and independent variables were developed from WMU specific information on tags issued for bulls and cows and two datasets on moose and moose hunters. The moose dataset included aerial survey counts of moose for WMUs. Flights with fixed-wing aircraft or helicopters are conducted annually for a sample of WMUs. The flights consist of multiple plots that are 2.5 by 10 km in size each (Oswald 1998). For reasons such as weather, the plots surveyed for a WMU in any year might be few in number. Therefore, only bull-, cow- and calf-moose populations estimated from at least 17 plots for a WMU in any year were included for the study. An OMNR regional biologist with years of experience working with the moose aerial-inventory data recommended using data from WMUs with at least 17 plots, to avoid including unreliable estimates of moose population into the sample. Because all WMUs are not surveyed every year and the estimated moose populations are subject to sampling error, the moose population estimates for each WMU were averaged from 1999 to 2010. The use of an average population size ensured that each WMU estimate was based on at least two and as many as five different years of population estimates.

The hunter dataset relied on a postcard survey completed by a sample of moose hunters from 1999 to 2010. The postcard survey is sent each year to all hunters who were successful in receiving an adult-moose validation tag (AVT). The survey is also sent to a sample of the hunters who were unsuccessful in receiving an AVT. For the WMUs in the present study, the annual average numbers of surveys issued from 1999 to 2010 were ~13 000 and 33 000 for AVT holders and unsuccessful-draw applicants, respectively. The average annual response rates were ~65% and 48%, respectively, for these samples. An existing database of these surveys that provided estimates of moose harvest for bulls, cows and calves by resident hunters, along with estimates of number of hunters and hunting pressure (days hunted) at the WMU level, was used. For each year and WMU in the present study, the average relative standard errors (i.e. standard error divided by mean estimate) were 10.6%, 15.8% and 38.0% for bull, cow and calf harvests, respectively (median relative standard-error estimates were 8.0%, 11.2%, and 34.7%, respectively). To reduce these relative standard errors and make the data compatible with moose population estimates, the harvest estimates were reported as average annual harvests from 1999 to 2010.

The dependent variables were the average annual tag-fill rates for bull and cow moose and the average annual proportion of calf population that was harvested. The tag-fill rates were calculated from the average annual number of projected bull (cow) kills divided by average annual number of bull (cow) tags issued for each WMU. Tags issued to and moose harvests estimated for tourism operators were excluded because the focus here was to understand actions of resident hunters. A tourist trip for hunting moose is likely to involve different considerations than other hunting trips. Although both resident gun and archery tags were included, most of issued tags were for gun hunting (90% and 82% of issued bull and cow tags, respectively). Proportion of calf population harvested equalled the average annual calf harvest divided by average annual calf population for each WMU.

The independent variables included themes of tag availability (reverse of scarcity), hunting opportunities, moose abundance and hunting pressure. Tag availability was measured in three ways. First, success rate of hunting applicants receiving a tag was calculated as the average annual number of tags issued, divided by the average annual number of tag applicants for each WMU. This general variable measured the difficulty for hunters to receive any AVT in a WMU. The other two measures of tag availability were WMU specific-density measures, with one being based on the average annual bull (cow) tags issued per km^2 of public lands available for moose hunting and the other on the average annual bull (cow) tags issued per km of wide roads (highway and designated primary and branch gravel-surfaced roads) on these public lands. The measure for land area concentrated on lands that would be available for hunting by all residents. Wide roads were measured rather than all roads because inventories for wide roads are better than inventories for single-lane gravel roads (e.g. some single-lane roads are not drivable). These measures of public land area and wide roads served to assess whether hunters were influenced by the availability of the geography of the WMU rather than by hunters in the WMU.

Hunting opportunities were crudely measured as road density (i.e. km of wide roads on public lands divided by km^2 area of public lands). This measure accounted for the ability of hunters to access the WMU by automobile. Moose abundance was measured as a density, in the following two ways: by km^2 of public land and by km of wide roads on these lands. Finally hunting pressure (i.e. projected days hunted in a WMU) was used as an independent variable for the calf harvest model. Hunting pressure was a density-based measure of days hunted with specifications by area (km^2 of public lands) and roads (km of wide roads on public lands).

Ten competing models were assessed for explaining variations in the average annual bull and cow tag-fill rates and seven models for explaining variations in average annual proportion of calf population harvested (Table 1). These models were selected to assess the importance of different measures of tag scarcity and calf abundance (density) and were not selected to test each independent variable separately.

The dependent variables were based on averages from several years, with different numbers of observations within and between each WMU. Therefore, it was not appropriate to estimate the model with a logistic regression. Instead, a logit-transformation ($\log(P/(1-P))$, where P is the probability) was conducted on all dependent variables (Warton and Hui 2011). No adjustment to the logit-transformation was necessary because all observations were less than one and greater than zero. Analyses were conducted with basic linear regression techniques. Heteroscedasticity was tested with a Breusch–Pagan statistic (Breusch and Pagan 1979) and when present ($P < 0.05$), heteroscedasticity-consistent standard errors were used (White 1980). The results section provides information on model selection, along with parameter estimates and standard errors for models with some support, defined here as a >10% chance of being the best model, given the set of competing models and the data (i.e. $\omega > 0.10$). Goodness-of-fit was based on an adjusted R^2.

Results

The 46 WMUs in northern Ontario varied markedly by environment, infrastructure, moose, AVTs and hunters (Table 2). The average WMU had less than 10 000 ha of public lands available for hunting and over 1000 km of wide (two-lane) roads on these lands. Average annual tag-fill rates for bull moose were slightly higher than those for cow moose (i.e. ~40% and 36%, respectively). The average annual proportion of

Table 1. Alternate models tested to understand average annual tag-filling rates and average annual proportion of calf population harvested in wildlife management units in northern Ontario, Canada, from 1999 to 2010

Model	Tag availability	Accessibility	Abundance	Hunting activity
Bull (cow) tag fill rate				
bull_0 (cow_0)	Null	Null	Null	Null
bull_1 (cow_1)	Tag success			
bull_2 (cow_2)	Tag success	Road density	Bulls (cows) area^{-1}	
bull_3 (cow_3)	Tag success	Road density	Bulls (cows) road^{-1}	
bull_4 (cow_4)	Tags area^{-1}			
bull_5 (cow_5)	Tags area^{-1}	Road density	Bulls (cows) area^{-1}	
bull_6 (cow_6)	Tags road^{-1}			
bull_7 (cow_7)	Tags road^{-1}	Road density	Bulls (cows) road^{-1}	
bull_8 (cow_8)		Road density	Bulls (cows) area^{-1}	
bull_9 (cow_9)		Road density	Bulls (cows) road^{-1}	
Calf harvest rate				
calf_0	Null	Null	Null	Null
calf_1			Calves area^{-1}	
calf_2			Calves road^{-1}	
calf_3		Road density	Calves area^{-1}	Hunting pressure area^{-1}
calf_4		Road density	Calves road^{-1}	Hunting pressure road^{-1}
calf_5		Road density		Hunting pressure area^{-1}
calf_6		Road density		Hunting pressure road^{-1}

Table 2. Descriptive statistics for variables describing moose populations, moose hunters and characteristics for 46 wildlife management units in northern Ontario, Canada, averaged on yearly basis from 1999 to 2010

Total moose abundance exceeds estimates from bulls, cows and calves as the sex and age of inventoried moose cannot always be determined

Label	Explanation	Mean	s.d.	Median
Bull tag-fill rate	Proportion of issued bull-moose tags	0.404	0.142	0.450
Cow tag-fill rate	Proportion of issued cow-moose tags	0.364	0.148	0.395
Calf harvest rate	Proportion of calf population harvested	0.147	0.088	0.139
Area	Area of WMU on public lands (km^2)	9265.857	7321.590	8101.559
Road	Total length of roads on public lands (km)	1030.479	651.595	931.986
Tag success	Proportion of applicants receiving an adult validation tag (AVT)	0.228	0.182	0.204
Tags $area^{-1}$	Issued AVTs by public lands (km^2)	0.045	0.056	0.030
Tags $roads^{-1}$	Issued AVTs by wide (two lane)-road length (km)	0.389	0.435	0.261
Road density	density of roads (km/area km^2)	0.218	0.510	0.131
Bulls $area^{-1}$	Bull density by area (km^2)	0.179	0.740	0.067
Bulls $road^{-1}$	Bull density by wide-road length (km)	0.703	0.675	0.484
Cows $area^{-1}$	Cow density by area (km^2)	0.266	0.963	0.118
Cows $road^{-1}$	Cow density by wide-road length (km)	1.004	0.559	0.879
Calves $area^{-1}$	Calf density by area (km^2)	0.075	0.239	0.037
Calves $road^{-1}$	Calf density by wide-road length (km)	0.358	0.274	0.283
Hunting pressure $area^{-1}$	Hunting pressure (days/area km^2)	2.260	3.910	1.431
Hunting pressure $road^{-1}$	Hunting pressure (days/wide-road length km)	12.724	8.445	9.372

harvested calf population was estimated at ~0.15. The average tag availability was ~23% of hunters applying for a tag actually receiving a tag. When compared with the available hunting area, 0.045 tags were available for every km^2 of public land available for hunting (i.e. one tag was available for approximately every 22 km^2). Likewise, on average, for every 1 km of wide roads on public lands, 0.39 tags were available (or roughly one tag for every 2.5 km of wide roads). Moose densities for bulls, cows and calves were generally highest for cow and lowest for calf moose, although considerable variability existed among the WMUs. Hunting pressure had an average of over two hunter days per km^2 on public lands for hunting or over 12 hunter days per km of wide roads, with considerable deviation around these averages among the WMUs.

The evidence for models explaining tag-fill rates for bull and cow moose was similar (Table 3). For both cases, the model with the minimum AICc included the success of hunters at receiving AVTs, the density of roads, and the density of bull or cow moose per km of wide roads. For bull-moose tag filling, the evidence for this model (bull_3) was very high ($\omega = 0.97$) and resulted in a high goodness-of-fit (adjusted R^2 of 0.75). For cow-moose tag filling, both the evidence ($\omega = 0.59$) and fit (adjusted $R^2 = 0.58$) were lower for this model (cow_3). In fact, some evidence ($\omega = 0.41$) supported the Model cow_7, which included the number of AVTs per km of wide roads, density of roads, and the density of cow moose per km of wide roads.

Of the seven competing models that were estimated to explain the average annual proportion of calf population harvested in each WMU (Table 4), the Model calf_4 had very strong evidence ($\omega = 0.97$) and a reasonable goodness-of-fit measure (adjusted $R^2 = 0.62$). This model included density of wide roads, density of hunting pressure by wide roads and density of calves per wide road.

The regression parameter estimates for all models with at least some evidence ($\omega > 0.10$) are illustrated in Table 5. Breusch–Pagan tests for heteroscedasticity were not significant for any of the models reported in Table 5 ($P = 0.09$, 0.89, 0.34 and 0.34 for Models bull_3, cow_3, cow_7 and calf_4, respectively). Consequently, heteroscedastic-consistent standard errors were not employed.

Table 3. Model selection results for averaged annual bull- and cow-moose tag-fill rate in wildlife management units in northern Ontario, Canada, from 1999 to 2010

LL = log-likelihood, k = number of parameters estimated, AICc = corrected finite sample Akaike information criterion, ΔAICc = difference in AICc from model with the lowest AICc and ω = probability of evidence for model given data and set of models

Model	LL	k	AICc	ΔAICc	ω	Adjusted R^2
Bull tag-fill rate (model)						
bull_3	–13.10	4	35.18	0.00	0.97	0.75
bull_2	–17.17	4	43.31	–8.13	0.02	0.70
bull_1	–20.19	2	44.67	–9.49	0.01	0.67
bull_7	–26.10	4	61.18	–26.00	<0.01	0.55
bull_5	–28.24	4	65.46	–30.28	<0.01	0.51
bull_6	–30.90	2	66.09	–30.90	<0.01	0.47
bull_8	–38.94	3	84.46	–49.27	<0.01	0.24
bull_9	–43.48	3	93.54	–58.36	<0.01	0.07
bull_4	–44.64	2	93.55	–58.37	<0.01	0.04
bull_0 (null)	–46.16	1	94.42	–59.23	<0.01	0.00
Cow tag-fill rate (model)						
cow_3	–31.58	4	72.14	0.00	0.76	0.58
cow_7	–31.95	4	72.88	–0.74	0.22	0.57
cow_2	–36.18	4	81.33	–9.19	0.01	0.48
cow_6	–40.62	2	85.52	–13.37	<0.01	0.40
cow_1	–40.69	2	85.65	–13.51	<0.01	0.40
cow_5	–39.26	4	87.49	–15.34	<0.01	0.41
cow_8	–42.99	3	92.54	–20.40	<0.01	0.32
cow_9	–44.19	3	94.95	–22.80	<0.01	0.29
cow_0 (null)	–52.97	1	108.02	–35.88	<0.01	0.00
cow_4	–52.93	2	110.14	–38.00	<0.01	0.00

Table 4. Model selection results for averaged annual proportion of calf population harvested in wildlife management units in northern Ontario, Canada, from 1999 to 2010

LL = log-likelihood, k = number of parameters estimated, AICc = finite sample-corrected Akaike information criterion, ΔAICc = difference in AICc from model with the lowest AICc and ω = probability of evidence for model given data and set of models

Proportion calf harvest	LL	k	AICc	ΔAICc	ω	Adjusted R^2
calf_4	–30.45	4	69.88	0.00	0.99	0.62
calf_6	–36.36	3	79.30	–9.42	0.01	0.52
calf_5	–42.38	3	91.33	–21.46	<0.01	0.37
calf_3	–41.91	4	92.80	–22.92	<0.01	0.37
calf_2	–49.56	2	103.40	–33.52	<0.01	0.16
calf_1	–51.76	2	108.19	–38.32	<0.01	0.07
calf_0 (null)	–54.11	1	108.21	–38.34	<0.01	0.00

For the tag-filling models (bull and cow moose), average annual tag success had a strong and negative effect. In fact, even without controlling for other variables, tag success was a good predictor of tag-filling rates for cow and bull moose (Figs 2, 3). The relationship between tag success and tag filling was stronger for bull than cow moose.

Average annual moose density (bull or cow) also was an important explanatory variable for explaining tag-fill rates. For all tag-filling rate models with some evidence, tag-filling rates increased with the density of bull or cow moose per km of wide roads. Road density also had a positive effect on the tag-filling rate for cow moose, whereas for bull moose, this effect, although positive, was relatively unimportant (i.e. low ratio of parameter estimate to standard error). Finally, for the cow tag-fill rate, some evidence also supported a model with a different measure of tag availability. The tag-fill rate for cow moose was negatively related to the density of AVTs per km of wide roads. This result suggested that as tags became scarce, hunters were better able to fill cow moose tags.

Only one model predicting the proportion of calf moose had some evidence, given the data and set of competing models. This model predicted positive relationships between the proportion of harvested calf population and road density and the hunter-effort density (days hunted per km of wide road). A strong negative relationship existed between calf harvest proportion and the density of calves on wide roads. This negative relationship suggested that as calf density declined, hunters took a larger proportion of the calf stock, *ceteris paribus*.

Discussion

The study was designed to answer two important questions for managing wildlife with a selective harvest system. The first question asked was how the availability of licences (tags) for bull and cow moose in WMUs relate to the success rate of hunters at filling these tags. The answer was that the tag-fill rate by moose hunters was negatively and strongly related to the availability of bull and cow tags to hunters. This negative effect held even when considering the density of bull and cow moose and the density of roads within WMUs. Apparently, in areas where tags are scarce, hunters who receive tags are better at harvesting moose than are hunters in areas where tags are less scarce. This relationship appeared stronger for filling bull- than cow-moose tags, suggesting a preference for harvesting bulls by northern Ontario hunters. This preference is consistent with Bottan *et al*. (2001) who found that about four times as many moose hunters in a part of northern Ontario preferred hunting bull to hunting cow moose.

At least two plausible explanations exist that could explain the relationship between tag abundance and the tag-filling rate. First, hunters might change their strategies for moose hunting as tags become scarcer. The analyses here did not permit an assessment of changing sophistication in strategies. However, other hunters have changed their strategies when resource and social conditions changed (e.g. Vaske *et al*. 2004; Alves *et al*. 2009). As illustrated by Fryxell *et al*. (2010), such responses by hunters should lag behind changes to resource and social conditions. Second, some hunters might cheat on rules as the availability of tags and moose decline. Therefore, hunters might be more successful in filling tags because they violate rules and norms while hunting moose. Indeed, Todesco (2004) reported that illegal moose kills in WMUs in north-eastern Ontario were positively associated with the number of tag applicants.

Regardless of the reason, attempting to reduce moose harvest through reductions to tags might result in hunter responses that increase their ability to fill tags. Consequently, this implementation uncertainty might trap managers, whereby wildlife populations are consistently exploited at higher than expected levels. Such a surprise that emerges from the coupled social-ecological system can jeopardise wildlife populations

Table 5. Regression parameter estimates for models with evidence (ω > 0.10) for averaged annual bull and cow tag-fill rate and average annual proportion of calf population harvested in northern Ontario wildlife management units from 1999 to 2010 (s.e. in parentheses)

Parameter	Bull tag fill-rate model (bull_3)	Cow tag fill-rate model (cow_3)	Cow tag fill-rate model (cow_7)	Calf harvesting-rate model (calf_4)
Intercept	0.022 (0.149)	–1.116 (0.244)	–1.255 (0.248)	–2.762 (0.244)
Tag success	–3.735 (0.345)	–2.531 (0.332)		
Tags road^{-1}			–1.082 (0.198)	
Road density	0.786 (0.634)	3.666 (0.826)	3.390 (0.781)	3.136 (0.939)
Bulls road^{-1}	0.391 (0.090)			
Cows road^{-1}		0.521 (0.128)	0.543 (0.153)	
Calves road^{-1}				–1.080 (0.308)
Hunting pressure road^{-1}				0.060 (0.009)

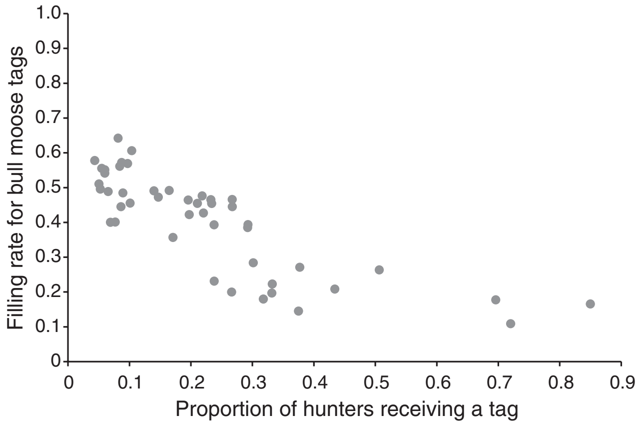

Fig. 2. Scatter plot of average annual availability of adult validation tags for moosed (proportion of hunters receiving a tag) and the average annual filling rates for bull-moose tags, respectively, for wildlife management units in northern Ontario, Canada, from 1999 to 2010.

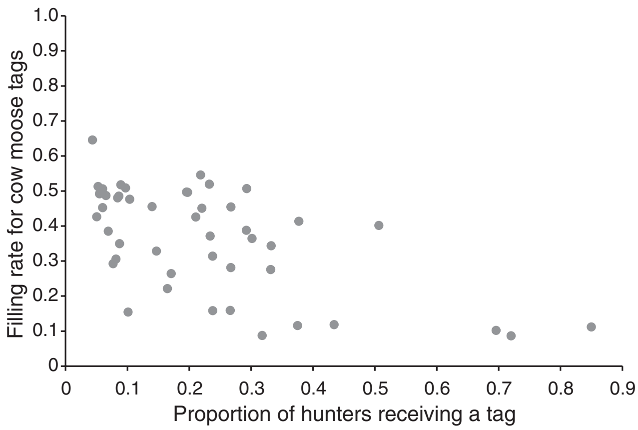

Fig. 3. Scatter plot of average annual availability of adult validation tags for moose (proportion of hunters receiving a tag) and the average annual filling rates for cow-moose tags, respectively, for wildlife management units in northern Ontario, Canada, from 1999 to 2010.

and encourage wildlife managers to apply additional restrictions on moose hunting. These additional restrictions could result in further changes to hunter strategies and harvest success. Furthermore, exposing hunters increasingly to restrictive regulations might undermine support for regulations and the management agency.

The second question asked was how hunting pressure and the relative abundance of calf populations within a WMU relate to the harvest rate of the calf population. The answer was that a moderate but important negative effect existed between the rate of calf-moose population harvested and the calf density, even after accounting for hunting pressure. This result suggests, *ceteris paribus*, that as the calf density declines, the rate of calf population that is harvested increases. This depensatory effect on calf populations implies that without understanding hunters, managers can become trapped in situations where declines to calf populations result in relatively greater harvest rates of calves.

This result is similar to an inverse density-dependent harvest effect that has been suggested for moose (Bowyer *et al*. 1999). Inverse density-dependent harvests signal that hunters become increasingly efficient predators as populations decline. This ability of hunters to maintain their hunting success as populations decline causes at least two problems for managers.

First, many hunters will base their assessment of wildlife populations on their hunting success. Consequently, if wildlife populations decline at a different rate than does hunting success, hunters might disagree with wildlife managers about the state of the resource. This can result in a conflict, whereby hunters react negatively to any regulatory change designed to increase wildlife populations. The disconnect between wildlife population and harvest success might also prevent hunters from traveling elsewhere to find hunting opportunities where game is more abundant, resulting in increased potential for population collapses in areas near hunting residences (*sensu* Hunt *et al*. 2011).

Second, resource management agencies who track wildlife populations through hunter-reported harvests might be unaware that wildlife populations are approaching critical thresholds that could greatly affect populations. Given concerns about the financial costs associated with aerial counts of wildlife populations, interest in enumerating wildlife populations from harvest data from hunters is increasing (Boyce *et al*. 2012). If inverse density-dependent harvest effect exists for wildlife, inferring estimates of wildlife populations from hunter success can be highly misleading.

The effects of other variables in the models generally followed intuition. For the models of tag-fill rate, road density had a positive, yet very weak, effect on the fill rate. Likewise, moose density had a moderate and positive effect on tag filling, suggesting that declining moose density reduces the ability of hunters to fill their tags. This relationship lessens, but does not reverse, the effects of tag scarcity on tag-filling rates. For the calf harvest model, road density and hunting pressure had moderate to strong positive effects, suggesting that as WMUs become increasingly accessible to hunting populations, the proportion of calf harvests increase. This result is consistent with findings of other studies, which have noted that accessibility of hunting areas is associated with increased harvests (Schmidt *et al*. 2005). As expected, hunting pressure had a significant effect on the harvest rate of calves. Therefore, in areas near human settlements, additional restrictions might be necessary to sustain calf and ultimately moose populations. This effect is recognised in Ontario, whereby calf harvests in some heavily hunted WMUs in southern Ontario are subject to a tag harvest system (OMNR 2012).

The information from the present study has illustrated the potential for managers to be provoked into traps of developing and implementing increasingly restrictive regulations, only to see hunters respond with strategies that result in higher than expected harvests. This potentially surprising result from the coupled social-ecological system for wildlife management can result in unsustainable harvests of wildlife or an escalation of regulations that can undermine the social goals for wildlife management. Cox and Walters (2002) termed a similar result in recreational fishing as ‘success breeds failure’, whereby recreational fishers respond to changing resource conditions in a way that undoes any catch-related quality improvements in fish populations from management actions. Managers and hunters should encourage and embrace research that seeks to understand how hunters respond to changing resource and social conditions (Prukop and Regan 2005). Armed with a better understanding of the hunter and implementation uncertainty, managers can better predict how different regulations are likely to affect the actions of the hunter (Stedman *et al*. 2004).

The presented study would benefit from replication and further investigation into the causal mechanisms for the observed responses of hunters to changing social and resource conditions. Understanding the casual mechanisms will require specific information about hunter strategies and behaviours.

Conclusions

Managing wildlife involves managing people. Although a cliché to some, it is hoped that other readers will view this and related research as signalling the importance of understanding hunters and their actions for effective wildlife management. The responses of hunters to changing social (tag availability) and resource (calf abundance) conditions illustrate the importance of understanding hunters.

When the availability of tags required for hunting bull and cow moose decreased, hunters had higher rates of filling these tags. As calf-moose populations decreased, hunters took a larger proportion of the stock of calf moose. These two results suggest that the design of rule-based institutions must consider the responses of hunters. Without understanding the coupling of social-ecological systems and the feedbacks from changing resource and social conditions on wildlife, managers can be surprised to find that hunters harvest at rates higher than expected. Only by using studies about hunters to reduce implementation uncertainty can rule-based institutions be designed efficiently and effectively, so as to manage wildlife and benefit hunters.

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