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Test of precipitation, compensation and Monday effect hypotheses on group hare trapping effort

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Live trapping in combination with translocation of wild animals is an important tool in wildlife management, but drivers of human trapping activity are poorly understood. Here we test three hypotheses that have been proposed to describe and explain temporal variation in group hunting-trapping effort. Namely, we test the precipitation effect, effort compensation and Monday effect hypotheses on live trapping effort of brown hares for restocking. Analysis of 26 047 hares trapped in 460 trapping days during the period 1966–1995 in western Poland showed that seasonal onset of trapping was later during rainy autumns supporting avoidance of rainy weather by the trapping group. The hunting group increased the number of animals caught the day following a day with low off-take providing evidence for the ability to respond quickly and compensate for short term variation in the trapping effort. Group trapping effort as reflected by number of hares caught was lower on Monday than on any other working day. This is in line with observations on weekly variation in working effort of employees across various contexts. We conclude that even seemingly standardized and rigid trapping schemes may be responsive to factors such as weather, experienced effort and subtle seasonal effects.

Economic incentives are among the most common drivers of human harvesting behaviour (Langenau et al. 1981, Clark 1990, Milner-Gulland and Leader-Williams 1992, Wam et al. 2012b). The amount of time hunters devote to hunting, when and where they hunt and number of killed animals they end up with is determined by spatio-temporal variation in current and even past density of prey (van Deelen and Etter 2003, Smith et al. 2005, Fryxell et al. 2010, Willebrand et al. 2011). In recreational hunters non-consumptive activities such as experiencing nature and seeing wildlife may provide more satisfaction than the simple acquisition of a natural product (Hammitt et al. 1989, Tynon 1997, Schwabe et al. 2001, Wam et al. 2012a, Vaske and Roemer 2013).

The precipitation effect hypothesis predicts that precipitation negatively affects the decision of a recreational hunter to hunt (Tynon 1997, Schwabe et al. 2001, Rivrud et al. 2014). The effort compensation hypothesis predicts that recreational hunters compensate for low trapping effort in the current hunting session by increasing trapping effort in the next session (Fryxell et al. 2010). Recreational hunters' typically hunt during the weekend or holidays when they have time off from work, but our understanding of daily variation in hunting effort is far from complete (Rivrud et al. 2014). It remains less clear to what degree the above hypotheses may explain temporal variation in hunting effort of a group when flexibility of most group members may be severely constrained. For example, several hired workers may join in live trapping of a larger number of animals, but the trapping activity is ultimately controlled by a few superiors.

In Poland, live trapping with net enclosures has been applied in the conservation and management of the brown hare *Lepus europaeus* (Andersen et al. 2009, Stamatis et al. 2009, Spyrou et al. 2013). The primary aim of live trapping has been to capture and relocate hares to areas with low hare density. In the 1960–1990s many thousands of hares were live trapped with nets by various trapping groups across Poland and translocated nationally or sold primarily to France and Italy (Jezierski 1968). The importance of trapping decreased over the years as hare populations started to decline in late 1970s and eventually crashed in the 1990–2000s and never fully recovered (Smith et al. 2005, Kamieniarz and Panek 2008, Panek 2013). The Europe wide decline in hare populations has been ascribed to habitat deterioration as well as an increase in predator and disease pressure (Smith et al. 2005, Kamieniarz and Panek 2008, Meichtry-Stier et al. 2014). Recently, fewer than 500 hares are live-trapped annually in Poland (Kamieniarz and Panek 2008).

Here we explore proximate factors of temporal variation in group brown hare trapping effort in an extensive dataset from a trapping ground in western Poland. Specifically, we test the prediction of the precipitation effect hypothesis that hare trapping starts later in the season if the weather is wet. Next, we test the prediction of the effort compensation hypothesis that the trapping group compensates for low trapping effort on one day by increasing trapping effort the next day. In addition, we test the Monday effect hypothesis that predicts that the trapping effort is lowest on Monday when motivation and tendency to work proactively are generally lowest during the working week (Fritz and Sonnentag 2005, van Hooff et al. 2007, Butler et al. 2014).

Material and methods

Study site

Hare trapping was conducted on the hunting grounds of the Research Station of the Polish Hunting Association located near Czempiń ('Research Station' hereafter), western Poland (52°08′N, 16°45′E) (Andrzejewski and Jezierski 1966, Hušek et al. 2015). The study area (150 km^2 until mid-1980s, 100 km^2 afterwards) was largely composed of arable land with only about 6–7% being covered by forests and woodlots sized between 0.5 and 2.7 km^2. Agriculture has been intensified from the mid-1960s to the mid-2000s. The proportion of the dominant crop, cereals, increased by ca 15%, wheat production doubled, and the area of uncultivated land covered with wild vegetation decreased (Panek unpubl.). Mean monthly number of days with snow cover was 2.6 in November, 11.0 in December, 15.9 in January and 12.2 in February during the years 1960/1961–1999/2000 (Bednorz 2009). The autumn density of hares, estimated by the belt census method (width 100 m and length of 50–60 km; Pielowski 1969), decreased at the study site (annual range 37.3–54.1 individuals per km^2 during 1965–1976, 16.6–26.3 during 1979–1990 and only 4.4–8.1 individuals per km^2 during 1999–2006) (Panek 2013).

Live net trapping of hares

Every year a trapping plan consisting of trapping quotas and the preliminary distribution of plots to be used for live trapping was decided prior to the hunting season by the head of the Research Station. The order in which plots were trapped was decided only after the actual trapping season started. The official beginning of the hare trapping season was the 1 November during the years 1965–1970, the 1 October (1971–1975), the 15 October (1976–1994) and then again the 1 November afterwards. The hunting season officially ended by 10 January (1965–1971), 31 January (1971–1994) and by 15 January afterwards.

The trapping group was composed of approximately 40 people, from which about 10 members were employees of the Research Station and the rest were local people hired for different time periods. The core members of the trapping group that were permanent employees of the Research Station remained largely the same over the years, but the composition of local people hired for helping in hare trapping varied. Square or polygonal plots were fully enclosed by nets and surrounded by ca. 20 hare collectors (Andrzejewski and Jezierski 1966). After the nets were raised and collectors stationed at their posts, ca 20 people beating the ground with wooden sticks walked through the enclosed plots four times and flushed hares into the nets where they were collected into wooden boxes. About 70% of all hares present inside the enclosure were trapped by nets. The rest managed to escape before the plots were enclosed (ca 10%), escaped from the nets (ca 10%) or remained in the plot (ca 10%) (Pielowski 1969, Pinkowski 1995). The number of plots enclosed on each day of trapping tended to increase from 2–3 to 3–4 over the season as experience and efficiency of the trapping group improved. Each plot was enclosed only once during a trapping season. Size of the enclosed plots decreased over the years from about 1.2 km^2 in the early 1960s (Andrzejewski and Jezierski 1966) to about 0.7 km^2 in the late 1980s (Pinkowski 1995).

According to the official trapping reports on average 16% (range 1–30%) and 2% (range 0–8%) of estimated autumn hare population size within the study site was taken off annually by trapping and shooting, respectively. In total 26 790 hares were captured with nets during the trapping seasons 1965/1966–1994/1995 from which 25 308 hares were used for restocking in other populations and the rest were released back in the study area as a part of studies on hare ecology (Jezierski 1968, Pielowski 1971, Hušek et al. 2015). In this study we analyse the available daily trapping records on 26 047 hares captured during 460 daily trapping sessions. Daily trapping records were not available for the seasons 1990/1991 (official trapping records were lost) and 1980/1981 (no hare trapping was conducted).

Precipitation data

Data on monthly precipitation (mm) during the trapping season for the period 1970–1994 were obtained from the Borowo meteorological station located in the centre of the experimental area. We defined November–December and January–February as the months that best reflected weather conditions at the beginning and at the end of the trapping season, respectively (Fig. 1a).

Statistical analyses

To test the precipitation effect hypothesis we fitted two linear models. In one model we considered the first date in the season when the trapping group was out trapping ('first trapping date') as a response variable and year and precipitation in November-December as continuous explanatory variables. In the other model we considered last date in the season when the group was out trapping ('last trapping date') as a response variable, and year and precipitation in January–February as continuous explanatory variables. Residual terms were correlated in both models (Durbin–Watson statistics > 1.1, $p < 0.04$). We modelled correlation structure of the residual terms in both linear models by an autoregressive process of order 1 (AR1) which allowed us to account for non-independence between a residual term in one year and a residual term in the following year. The linear models with AR1 structure for residual terms were fitted using generalized least squares (gls) implemented in the library nlme, ver. 3.1-117 (Pinheiro et al. 2015) in R, ver. 3.1.1 (<www.r-project.org>). Calendar dates were transformed to Julian dates (1 = 1 January).

To test the effort compensation hypothesis we specified a single linear mixed effect model where the difference in the number of trapped hares between two consecutive trapping days ('change in following day off-take') was included as an

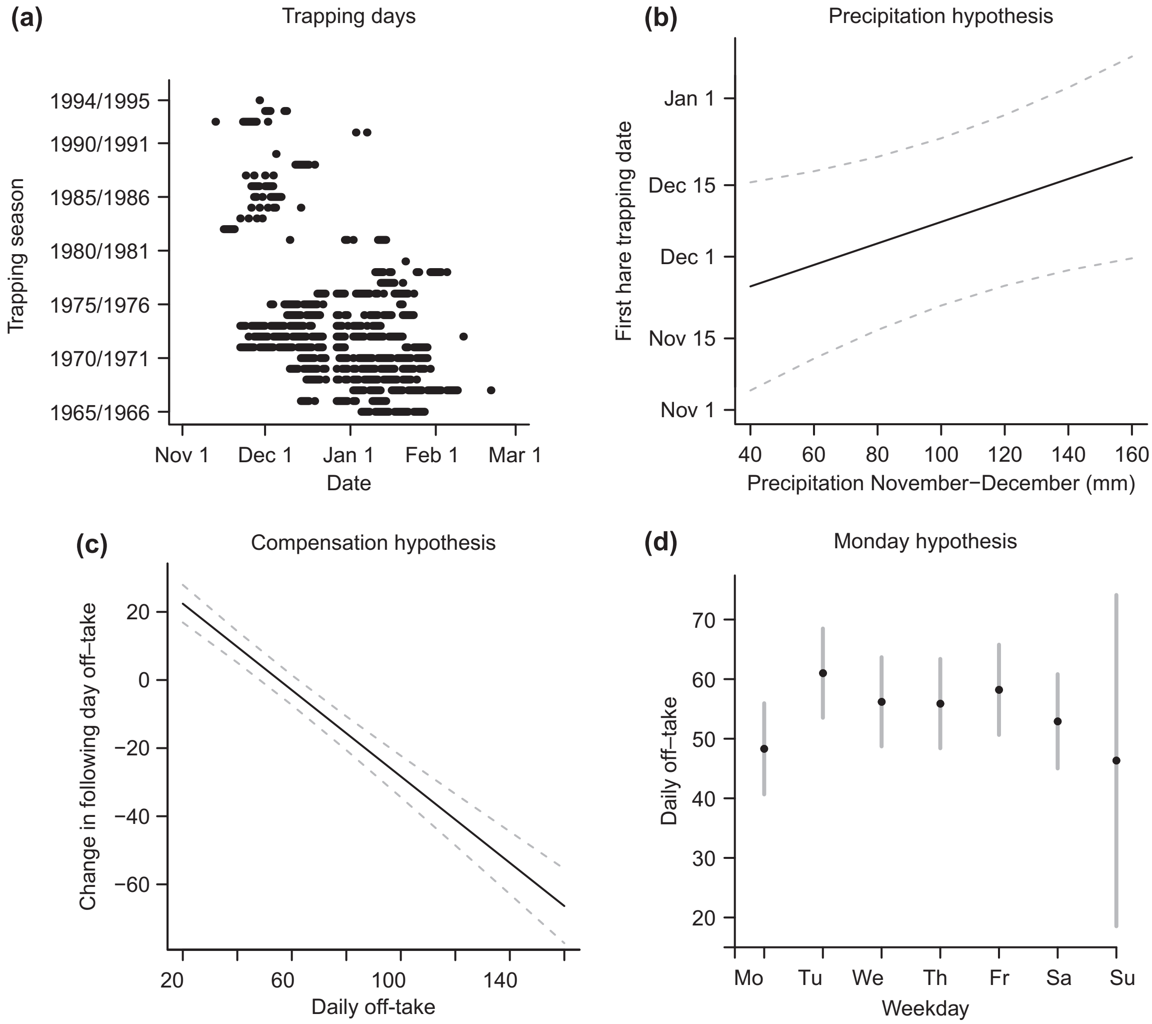

Figure 1. Results of analyses on the brown hare group trapping activity in western Poland during the seasons 1965/1966–1994/1995: (a) Seasonal distribution of days the trapping group was out trapping. (b) The effect (± 95% CI) of precipitation in November–December on the first day in the season the trapping group was out trapping. (c) The effect (± 95% CI) of the number of hares trapped on a given day (daily off-take) on the change in the number of trapped hares to the following trapping day (change in following day off-take). (d) Variation in the mean number (± 95% CI) of trapped hares (daily off-take) during the week.

response variable and the number of trapped hares on the previous day ('daily off-take') was included as a fixed explanatory factor. The effect of year was included as a random effect. We used a randomization test to evaluate whether the model fit was influenced by the fact that the change in following day off-take can only be positive/negative at the very low/high value of daily off-take, respectively (Manly 2007). The effect of the daily off-take on the change in following day off-take estimated from the data was compared with a distribution of estimates obtained by running 1000 mixed effect models, all of which had the same structure of explanatory factors and only differed in that the value of the change in following day off-take (response variable) for each model was randomly drawn from a set of all possible values from a given year.

To test the Monday effect hypothesis we specified a linear mixed effect model where we included daily off-take as a response variable, categorical effect of weekday as a fixed explanatory variable and the effect of year as a random effect. In the mixed model we detected significant serial correlation of the residuals at lag 1 and 2 from the correlogram. Hence, we report the fit of the linear mixed effect model where the correlation structure of the residual terms was approximated by AR1 which was supported over the original mixed effect model without any correlation structure of the residuals (likelihood ratio test, $\chi^2_1 = 48.9$, $p < 0.001$).

All mixed effect models were fitted by REML except in the likelihood ratio test where fit by ML was favoured. We used function lme of the library nlme to fit the mixed models (Pinheiro et al. 2015). We checked the normality of residuals and constancy and homogeneity of variance and concluded that assumptions of the mixed models were not violated (Pinheiro and Bates 2000).

Results

Test of the precipitation effect hypothesis

The first trapping date did not change over the years , but it was 2.1 days later in the season with every 10 mm increase in precipitation in November–December ($\beta_{year} = -0.41 \pm 0.95$, $t = -0.43$, $p = 0.67$, Fig. 1a; $\beta_{precipitation} = 0.21 \pm 0.09$, $t = 2.30$, $p = 0.03$, $n = 23$, Fig. 1b). The negative effect of precipitation in January–February on the last trapping date was not statistically significant, but the last trapping date advanced over the study period, every year being earlier by 2.6 days ($\beta_{year} = -2.60 \pm 0.74$, $t = -3.51$, $p = 0.002$, Fig. 1a; $\beta_{precipitation} = -0.16 \pm 0.09$, $t = -1.79$, $p = 0.09$, $n = 23$).

Test of the effort compensation hypothesis

Change in following day off-take was negatively related to the daily off-take (fixed effect: $\beta_{off\text{-}take} = -0.63 \pm 0.05$, $DF = 406$, $t = -13.04$, $p < 0.001$; random effects: $SD_{year} = 8.0$, $SD_{residual} = 25.7$; $n = 432$; Fig. 1c). The estimate of the slope (–0.63) fell completely outside of the distribution of slope estimates derived by randomization, thus rejecting the hypothesis that the effect of daily off-take on change in following day off-take was generated by random variation ($p < 0.001$).

Test of the Monday effect hypothesis

Daily off-take was lower on Monday than on any other working day (Table 1, Fig. 1d).

Discussion

Hunters adjust hunting effort in relation to environmental variation, prey density, motivation and satisfaction, but the strength of the response to each of the above factors vary greatly between recreational hunters hunting primarily for leisure (Wam et al. 2012a, Haugen et al. 2015), indigenous hunters hunting mainly for food (Lee and DeVore 1968), and hunters or poachers hunting or fishing for economic profit (Milner-Gulland and Leader-Williams 1992, Jahren 2012). We show that the effects of precipitation, experienced number of trapped hares and day of the week all affected either the onset of the trapping season or the daily off-take of hares in a trapping group in western Poland.

The precipitation effect hypothesis

The first trapping day was later in years with higher precipitation in November–December. Ultimately this reflects practical issues. Movement of trappers and their vehicles may be severely hampered on soaked agricultural crop fields and hare hunting bags may be negatively correlated with precipitation (Santilli and Galardi 2006). The effect of precipitation on the timing of trapping is likely underestimated in our study. This is because part of the variation in timing of trapping that could have been accounted for by precipitation data on a finer time scale (e.g. daily precipitation) likely went unexplained by the effect of precipitation approximated on a rather coarse time scale (i.e. precipitation in November–December). Indeed, change in a hunting strategy in response to unfavourable weather conditions is common. For example, indigenous hunters of the San of the central Kalahari stop using traps during the rainy season as trapped animals have a high chance of escaping from the trap in wet weather (Ikeya 1994) and the Bari Indians of Colombia and Venezuela switch from fishing to hunting when the former becomes unprofitable during the rainy season (Beckerman 1983). Miskito Indians of eastern Nicaragua go hunting during the rainy weather as animals trapped by floods are easier to kill (Nietschmann 1972). Though not statistically significant, the effect of precipitation in January–February on the last day the trapping group was out trapping was negative.

Table 1. Coefficients from the linear mixed effect model on the effect of week day, with Monday as the reference category, on the daily off-take of brown hares in the hunting ground in western Poland. Sample size $n = 460$ observations in 28 years, $DF = 426$.

Coefficient	Slope	SE	t-value	p	SD
Fixed effects					
Intercept	48.3	3.89	12.41	< 0.001	
Tuesday	12.7	3.47	3.66	< 0.001	
Wednesday	7.9	3.90	2.02	0.044	
Thursday	7.6	4.00	1.91	0.057	
Friday	9.9	3.95	2.51	0.013	
Saturday	4.6	3.68	1.25	0.210	
Sunday	−2.0	14.13	−0.14	0.900	
Random effects					
Year					11.13
Residual					26.74

The effort compensation hypothesis

Previous studies have provided evidence for the spatial, seasonal and inter-annual flexibility in hunters to compensate for low hunting yield. White-tailed deer *Odocoileus virginianus* and moose *Alces alces* hunters decreased their hunting effort, Swedish willow grouse *Lagopus lagopus* hunters, and the San of the central Kalahari changed to a new hunting location when game populations declined and bag size diminished (Ikeya 1994, Fryxell et al. 2010, Asmyhr et al. 2013). On the other hand, Texas hunters of scaled quail *Callipepla squamata* and northern bobwhite *Colinus virginianus* do not seem to harvest more than 12–15 birds on a given day irrespective of the bird density (Peterson 2001). Here we show that the hare trapping group was flexible enough to respond to its trapping effort on a much finer, daily scale.

Low trapping off-take on one day was compensated by a higher effort and so a higher off-take on the following date. Despite the evidence that the hare trapping effort was flexible from day to day, the underlying causality is not clear. Group trapping effort may have been altered both by daily changes in the size and composition of the group, number, size and exact location of trapping plots to be enclosed on a given day or a combination of these factors. Typically, the number of daily enclosed plots increased from 2–3 at the beginning of the season to 3–4 at the end of the season and the average size of the trapping plots decreased over the years (Andrzejewski and Jezierski 1966, Pinkowski 1995), but more detailed seasonal data are not available. The observation of a decrease in daily off-take following a day with high off-take is more difficult to explain. It is not clear why the trapping group did not attempt to steadily increase the daily off-take given the yield influenced pay. First, hare trappers may have sought sustainable trapping and viability of the local hare population. A steady increase in the off-take could hamper prospects for future economy income from trapping. Second, the trapping group may have been satisfied with high yield on one day and have been somewhat less motivated to continue high trapping effort the following day. Third, the group may have pre-emptively trapped at good sites first. Fourth, it may not have been possible to further increase daily off-take if it was already too high on the previous day. Results of the randomization test showed that the observed effect of daily off-take on the change in following day off-take was not simply a result of such trapping constraints.

The Monday effect hypothesis

Contrary to recreational hunters, who may go out hunting only when they have free time from their jobs and who have to pay various hunting fees, the hare trapping group was active during the working days only and the group members were hired for the job. It is perhaps not surprising that the lower daily off-take of hares on Monday compared to other working days conformed with the general pattern of weekly variation in working effort commonly observed in other contexts (Fritz and Sonnentag 2005, van Hooff et al. 2007, Butler et al. 2014).

Again, our data did not allow us to distinguish whether workers were less motivated to work on Monday (in Poland, only Sunday was a free day until 1981 when Saturday was declared a free day three times a month) from other plausible explanations such as that the trapping group was smaller (workers quitting the job on Monday were only replaced by new and motivated workers on Tuesday) and/or enclosed plots were smaller and fewer on that day.

Management implications

The revival of live trapping as a tool for restocking of brown hares seems unlikely at present (Sokos et al. 2015). Yet, it is vital to realize that even seemingly standardized group trapping schemes, like the one described here are not as rigid as one may think and may be affected in the field by factors such as weather, past effort and subtle seasonal effects. Indeed, paid hunters may show patterns of activity that are quite different from those of recreational hunters. It would be instructive to better understand the causality of behaviour of hunting groups if the aim was optimization of hunting activities on the one hand and improvements in generation of a positive hunting experience for engaged group members on the other hand.

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