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Different hunting strategies select for different weights in red deer

María Martínez[1,*], Carlos Rodríguez-Vigal[2], Owen R. Jones[3], Tim Coulson[3] and Alfonso San Miguel[1]

[1]*E.T.S. Ingenieros de Montes, Ciudad Universitaria s/n, 28040 Madrid, Spain*
[2]*Centro "Quintos de Mora", Organismo Autónomo Parques Nacionales, c/ Costanilla de San Lázaro no. 3, 45003 Toledo, Spain*
[3]*NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berks SL5 7PY, UK*
**Author for correspondence* (*martinezmari@gmail.com*)

Much insight can be derived from records of shot animals. Most researchers using such data assume that their data represents a random sample of a particular demographic class. However, hunters typically select a non-random subset of the population and hunting is, therefore, not a random process. Here, with red deer (*Cervus elaphus*) hunting data from a ranch in Toledo, Spain, we demonstrate that data collection methods have a significant influence upon the apparent relationship between age and weight. We argue that a failure to correct for such methodological bias may have significant consequences for the interpretation of analyses involving weight or correlated traits such as breeding success, and urge researchers to explore methods to identify and correct for such bias in their data.

Keywords: *Cervus elaphus*; trophy-stalking; montería; management; bycatch; selection

1. INTRODUCTION

Considerable ecological and evolutionary insight may be derived from records of shot animals (Mysterud *et al.* 2001; Yoccoz *et al.* 2002; Bonenfant *et al.* 2003; Carranza *et al.* 2004). Although this approach often controls for age and sex, it is typically assumed that shot individuals represent a random sample of the particular demographic class to which the animals belong. However, hunting is often not a random process with hunters often selecting a non-random subset of the population (Noss 1999). A failure to understand and correct for bias introduced in this way may have important consequences for the correct interpretation of analyses of hunting data.

It is perhaps surprising that such corrections, although routinely carried out by fisheries managers (Murphy & Willis 1996), are rarely used in terrestrial population biology. This is despite the fact that many researchers have highlighted the influence that selective hunting may have on the population dynamics of the system they are studying (Ginsberg & Milner-Gulland 1994; Laurian *et al.* 2000) and are, thus, aware of the bias that exists in data sourced from hunts.

Given that red deer are often hunted for commercial purposes (as a trophy or for meat), or for conservation and management purposes, an important source of bias may be the objective of the hunt and the resulting selection for different characteristics. For example, in a commercial hunt, there may be selection for large antler or body size whereas in a management hunt the deer may be selected for small size or disease status. The introduction of such bias is likely not only to affect the apparent age, size or sex structure of the population but may also influence the apparent statistics of other traits such as antler size, body mass and disease status. The particular methodology used by the hunter, which varies across cultures, may also influence apparent population characteristics. Examples of such contrasting methodologies include solitary stalking, hunting in groups and hunting with or without dogs. It is likely that the efficiency (in terms of number killed) and selective bias of such hunts vary widely.

In this paper we use a dataset collected from 'Los Quintos de Mora', a ranch located in Toledo, Spain, to study the effect that one important source of bias, hunting type, has on the apparent functional relationship between age and weight in male red deer (*Cervus elaphus*). This unusual dataset is ideal for such a task because, unlike most hunting datasets, the methodology of the hunt is recorded along with sex, age and weight information. We demonstrate that, for this Mediterranean population, the method of hunting has a significant influence on the age–weight relationship and argue that a failure to correct for the bias introduced would produce spurious results in analyses made using the data.

2. MATERIAL AND METHODS

(a) *The dataset and study area*

The data used in this study were collected in Los Quintos de Mora, a 6864 ha fenced ranch located in Toledo, Spain and managed by OAPN (Organismo Autónomo de Parques Nacionales). The main human activity in this Mediterranean ranch is hunting, which occurs between September and February.

Here we use sixteen years (1988–2003) of data on the hunting of male red deer. This dataset includes information on the hunting method and the dates on which the animals were killed. The weight of the whole animal (to the nearest kilogram) and its age (estimated using two methods: by assessing tooth wear and by counting tooth rings) were also recorded.

A number of hunting types are used in the ranch, depending on the management objectives. We consider four of these hunting types: (i) *bycatch* is defined as non-target red deer caught by hunting dogs during hunting; (ii) *montería* is when deer are driven towards concealed hunters by dogs and dog handlers so that the hunters can attempt to shoot the best deer; (iii) *trophy-stalking* consists of a hunter choosing a target male because of its trophy value and then stalking it until he considers that he has an accurate shot with which to kill the deer; and (iv) *management hunting* is when hunters attempt to target 'poor quality' males (who may be diseased, smaller than average, etc.). This hunting type is used to reduce the deer population to carrying capacity within the ranch and to increase antler quality.

In age estimation, for the tooth ring method, the left I1 incisors were analysed by counting cementum growth rings either in Matson's Laboratory (USA) or by staff at the Los Quintos de Mora laboratory. This method is an accurate estimator of age (Grue & Jensen 1979). The tooth wear method is based on a predictable pattern of tooth exchange and wear that occurs in the deer. We followed the methods of Lowe (1967) with some modifications because the tooth infundibulum is not totally isolated in deer from Los Quintos de Mora until 10 years of age, instead of the eight years for the deer on Rum.

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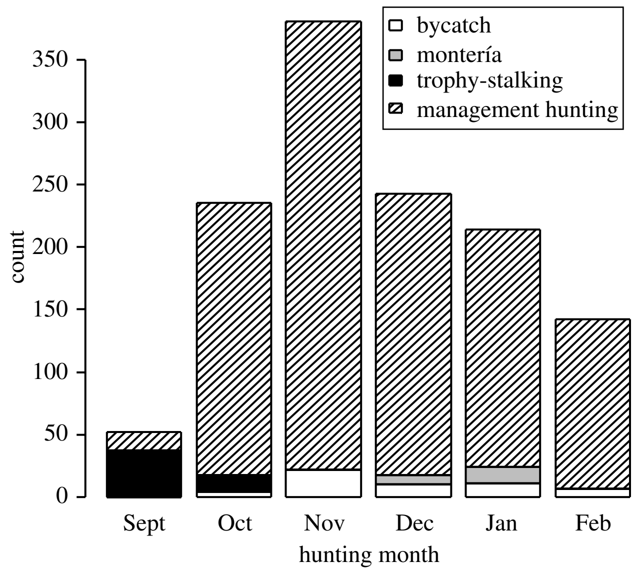

Figure 1. Number of animals shot between September and February (1988–2003) using each hunting type.

(**b**) ***Statistical methods***

A nonlinear least-squares regression model, using male data collected across all years (1988–2003), was constructed in order to characterize the weight of the hunted population, and to determine the effects of age (fitted as a continuous variable) and hunting type on weight.

To describe how weight changes as a function of age for each hunting type we fitted a family of asymptotic exponential curves to the data by obtaining least-squares estimates of the parameters *a*, *b* and *c* for each hunting type (equation (2.1)):

$$\text{weight} = a - b^{*}e^{(-c^{*}\text{Age})}|\text{hunting type}. \quad (2.1)$$

However, there are no data for young animals due to the nature of the monteria and trophy-stalking hunting types. Therefore, the curves were all forced to pass through the overall average weight of calves and, thus, a condition of the model was that $\text{weight}_{(\text{age}=0)} = 30.37 = a - b$.

Before analysis it was necessary to correct weight in order to account for the confounding effects of the month of the hunt (figure 1). We did this by adjusting the weights to what would be expected in November using a fully specified generalized linear model to model weight as a function of age and month, using a subset of 1145 males killed using management hunting ($r^2 = 0.831$).

We also corrected age to account for methodological differences in the age estimation techniques. To achieve a single estimate of age, age used in these analyses was defined as the tooth ring age (TR_{age}) where available, and was predicted from tooth wear age (TW_{age}) using a regression model when only TW_{age} was measured. The model used was: $TR_{age} = 0.945 \times TW_{age}$ ($r^2 = 0.963$, with a subset of 462 male and female individuals where age estimates were available from both methods).

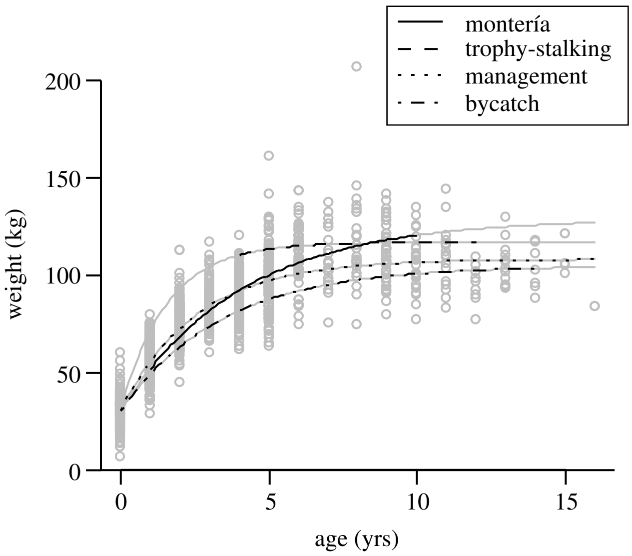

Figure 2. The relationship between age and weight for each hunting type considered in this study. The points represent empirical data while the lines show predictions for each hunting type from the nonlinear regression model (see table 1 for details). The ranges for which data are available are depicted with heavy lines, while areas for which we have no empirical data are shown with faint grey lines.

3. RESULTS

The nonlinear regression model explaining weight as a function of age and hunting type showed that there were significant differences in the weight–age relationships for animals killed using different hunting types (figure 2). The parameter estimates for the model, including the standard errors, are given in table 1.

These estimates are significantly different from each other when the 95% confidence limits of the estimates do not overlap. Using a pairwise comparison approach, we show that the parameter estimates for the four hunting types are significantly different in all cases except for the comparison for parameter *b* between the management and bycatch hunting types. Thus, the difference between the asymptote and the intercept (*b*; in most cases), and the slopes of the curve (*c*; in all the cases) are significantly different.

4. DISCUSSION

Bias is widespread in most ecological data, especially those collected by harvesting or hunting which are, by nature, selective (Ginsberg & Milner-Gulland 1994; Noss 1999; Laurian *et al.* 2000). Although introduced bias is routinely corrected for in fisheries systems (Murphy & Willis 1996), similar bias is often ignored in terrestrial systems. The present study, therefore, seeks to highlight this issue by using a hunting-derived dataset to examine the bias introduced by particular hunting methodologies.

Table 1. Parameter estimates for the nonlinear regression model explaining weight as a function of age.
(The coefficients are those that appear in equation (2.1) and describe the shape of the weight–age relationship curves. The four hunting types are described in §2. The model explains most of the observed variation in weight (nonlinear $r^2=0.830$). Residual standard error = 11.82 on 1260 d.f.)

coefficient	hunting type	estimate	s.e.m.	*t*-value	*p*-value
b	bycatch	74.53	4.61	16.17	<0.001
	montería	98.61	9.55	10.32	<0.001
	trophy-stalking	86.56	2.29	37.76	<0.001
	management hunting	77.89	1.11	70.00	<0.001
c	bycatch	0.29	0.05	5.90	<0.001
	montería	0.25	0.06	3.89	<0.001
	trophy-stalking	0.65	0.23	2.75	0.172
	management hunting	0.39	0.01	29.63	<0.001

Our results demonstrate that the hunting type used to collect the data has a significant influence upon the apparent relationship between weight and age. This bias is most pronounced (i.e. the differences between predicted weights for different hunting types are greatest) in young or adult deer rather than in very old deer. It is clear, therefore, that a hunter's objective has a significant effect on the characteristics of the shot animals and on selection pressure since larger animals are more likely to be shot at a younger age.

The objective of trophy-stalkers is to obtain the best (i.e. largest) trophy. Therefore, only adult animals (older than four years) are shot and there appears to be a threshold weight so that the weight of animals shot using this method changes little between four and twelve years of age. On the other hand, although montería hunters have the same aims as trophy-stalkers, they are apparently not as good at selecting for weight. This is probably because they are typically confronted with a larger number of animals that they can shoot but have less time to make an assessment and selection. Therefore, the animals they select are not as heavy as those shot using trophy hunting at young ages, and some young (less than 4 years) and small animals are shot, presumably in order to fill their quota. Finally, animals of every age are selected with bycatch and management hunting methods and, therefore, a more complete population sample may be possible. However, since both bycatch and management hunting tend to eliminate low-quality deer for every age, the sample is certainly not random. These selection pressures have clear consequences for wildlife management (Coltman *et al.* 2003).

When interpreting data collected by such an invasive method as hunting it is worth considering that simply the collection of the data can influence the system. In natural systems there is selection pressure to be large/heavy to ensure breeding success and survival (Saether 1997). Furthermore, in many systems anthropogenic hunting represents an additional source of selective pressure (Ginsberg & Milner-Gulland 1994; Laurian *et al.* 2000). The direction and strength of these pressures depend on the hunting methodology. For example, when management hunters shoot the weak/small individuals there may be a large positive selection on body mass. A more common situation in private Spanish ranches managed for profit, is that commercial hunting is more common than management hunting of males. It is clear that the balance of these natural and anthropogenic selection pressures may influence both the demographic structure and the dynamics of the system and should therefore be taken into account when comparing systems in different locations with differing selection pressures.

Although recent studies have shown that senescence occurs in red deer males above 10 or 11 years old (Mysterud *et al.* 2001; Carranza *et al.* 2004), we did not consider it in our analyses because 95.7% of the animals were under 11 years old. It is also pertinent to note that data were scarce for very young ages and, therefore, care should be taken not to over-interpret the model within these areas of parameter space.

Nevertheless, our results show that the apparent functional relationship between age and weight depends upon the methodology used to collect the data. Weight and body size are typically highly correlated and have a huge influence on individual fitness (Saether 1997). Clearly, bias introduced by a failure to control for hunting methods in the estimation of weight-related effects may have significant consequences for the interpretation of analyses involving weight or correlated traits such as breeding success (Clutton-Brock *et al.* 1982; Langvatn *et al.* 1996; Yoccoz *et al.* 2002; Bonenfant *et al.* 2003). We therefore urge researchers to explore methods to identify and correct for such bias in their data. We realize, however, that such bias may not be constant through time or space and, therefore, that correction over such scales may not be straightforward.

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