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PAPER

The use of a random regression model on the estimation of genetic parameters for weight at performance test in Appenninica sheep breed

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Abstract

The Appenninica breed is an Italian meat sheep; the rams are approved according to a phenotypic index that is based on an average daily gain at performance test. The 8546 live weights of 1930 Appenninica male lambs tested in the performance station of the ASSONAPA (National Sheep Breeders Association, Italy) from 1986 to 2010 showed a great variability in age at weighing and in number of records by year. The goal of the study is to verify the feasibility of the estimation of a genetic index for weight in the Appenninica sheep by a mixed model, and to explore the use of random regression to avoid the corrections for weighing at different ages. The heritability and repeatability (mean±SE) of the average live weight were 0.27±0.04 and 0.54±0.08 respectively; the heritabilities of weights recorded at different weighing days ranged from 0.27 to 0.58, while the heritabilities of weights at different ages showed a narrower variability (0.29÷0.41). The estimates of live weight heritability by random regressions ranged between 0.34 at 123 d of age and 0.52 at 411 d. The results proved that the random regression model is the most adequate to analyse the data of Appenninica breed.

Introduction

Collecting data for breeding programs of sheep populations living in harsh environment is difficult; particularly in meat sheep, where recording of growth data is limited to rams during the performance test (FAO, 2014; Sarti *et al.*, 2001): in such way the estimates of heritability are affected not only by the low number of observations, but also by the unreliable genealogy of females. Several authors estimated the genetic parameters of the growth traits in sheep through mixed model analysis, using both animal and sire models, and taking into account different fixed environmental factors (Atkins *et al.*, 1991; Borg *et al.*, 2009; Eskandarinasab *et al.*, 2010; Gowane *et al.*, 2011). When the age at recording is highly variable, the weights within a fixed range are usually adjusted to the same age, than the weight at different ranges are treated as separated traits (Brown *et al.*, 2000). The use of random regression (Meyer, 2004; Schaeffer, 2004) allows the overcoming of these limitations, since there is no need for age correction, so that the weights can be examined as one continuously changing trait, like weight actually is. Random regression models have been applied to estimate the genetic parameters in sheep (Fischer *et al.*, 2004; Lewis and Brotherstone, 2002; Molina *et al.*, 2007).

The Appenninica breed is an Italian meat sheep and it is mainly selected by morphology; however, a performance test procedure for rams started in 1986 and the weights of the young males are recorded monthly (Sarti *et al.*, 2001). The performance test lasts 10 months. Following the grazing availability, the lambs are reared in three different periods: at the beginning, they are reared indoor during the period February-May, then outdoor from June to September, and eventually indoor again in October-November; at the end of the test, the best males are approved as rams according to a phenotypic index. The index is calculated from the daily gains (ADG) between two consecutive weighing days: the ADGs are averaged within the rearing period, and then the performances in the three periods are weighted 2/7, 4/7 and 1/7 to get the overall index. The ASSONAPA (National Sheep Breeders Association) recorded the live weights of 1930 Appenninica male lambs, which were tested in performance station during 25 years: the increasing amount of weight recordings, and of genealogical information, could eventually give the chance to switch from a phenotypical evaluation to a real genetic index, estimated by a mixed model.

The goal of the study is to verify the feasibility of the estimation of a genetic index for weight in the Appenninica sheep by the comparison of different mixed models, and to explore the use of random regression to correct the effect of different ages at the weighing date. The results of this study can be useful not only to the Appenninica breed, but also in other meat sheep breeds that live in situations where data recording is affected by age variability.

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Key words: Selection; Variance component estimation; Meat sheep.

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Materials and methods

Since the data span from 1986 to 2010, there has been a huge variation in yearly climatic conditions: this variation affected the mating periods, so that the mean age at the beginning of the test changed in time, and also lambs tested in the same year did not start at the same age, because of the different geographical area of their origin. Furthermore, 10 weighing days should take places during the performance test: these operations are planned every 30 days, but there were important shifts, because seasonal conditions affected both the reproductive aspects of the ewes and the availability of handwork in the station.

The distribution of records per age (Figure 1) shows that lambs begin the test at very different ages, so that the highest frequency is only at 160 d: after this, it decreases because of the culling of lambs that do not reach a prefixed minimum weight. A filter was applied to remove animals that lost weight between two subsequent weighing (n=236) and animals coming from flocks with only one lamb (n=85). The filtered dataset contained 8546 weights of 1609 lambs from 73 farms (Table 1), and a pedigree file of 3552 animals treated by PEDIGREE WIEVER (ver. 6.4 b) was used for the analysis. Genetic connectedness was evaluated by means of average additive relationship within and between contemporary groups (r_{wCG} and r_{bCG}) and farms (r_{wF} and r_{bF}).

Four different statistical models were tested: in order to use any available information from the station test, slightly different datasets were analysed.

Model 1 (M1) was equivalent to an individual animal model with repeated records:

$$y = X\beta + Zu + Zp + Wf + e$$

where
y, was a vector of lamb weights;
β, was a vector of fixed effects including type of birth (single or twins), weighing day (182 levels), linear and quadratic regression on age;
u, was a vector of animal additive genetic effects;
p, was a vector of permanent environmental effects;
f, was a vector of farm random effects;
e, was the vector of random residuals;
X, was the incidence matrix for fixed effects;
Z, was the incidence matrix relating observations to animals;
W, was the incidence matrix for farm effects.
The (co)variances for random effects were:
$u \sim N(0; A\sigma_a^2)$
$p \sim N(0; I\sigma_p^2)$
$f \sim N(0; I\sigma_f^2)$
$e \sim N(0; I\sigma_e^2)$
where
A, was the additive genetic relationship matrix;
I, was an identity matrix.

Model 2 (M2) was a multiple trait individual animal model as follows

$$y_i = X_i\beta_i + Z_iu_i + W_if_i + e_i$$

where
y_i, was a vector of lamb weights at weighing day *i* (*i* = 1…10) during each test;
β_i, was a vector of fixed effects on trait *i* including type of birth (single or twins), testing year (from 1986 to 2010), linear and quadratic regression on age;
u_i, was a vector of animal additive genetic effects for trait *i*;
f_i, was a vector of random farm effects for trait *i*;
e_i, was the vector of random residuals for trait *i*;
X_i, was the incidence matrix of fixed effects for trait *i*;
Z_i, was the incidence matrix relating observations for trait *i* to animals;
W_i, was the incidence matrix of farm effects for trait *i*.
The (co)variances for random effects were:
$u \sim N(0; G)$
$f \sim N(0; R_f)$
$e \sim N(0; R_e)$
where
G, was the 10 by 10 additive genetic covariance

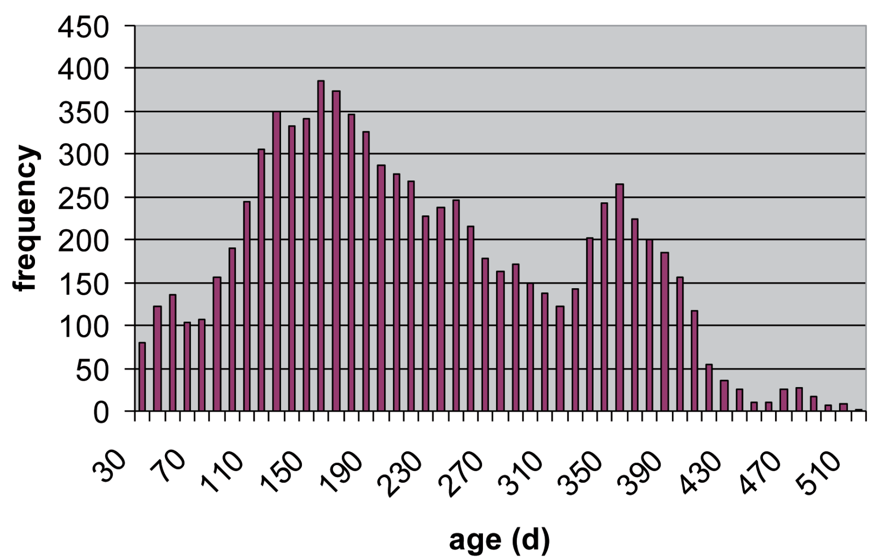

Figure 1. Frequency of the 8867 weights of Appenninica lambs registered at the performance test station from 1986 to 2010 by age of lambs at weighing.

Table 1. Statistics of weight and age according to weighing days during the performance test (n=8546; lambs=1609): dataset used in models M1 and M2.

Weighing day	N.	Weight, kg				Age, days			
		Mean	Min	Max	sd	Mean	Min	Max	sd
1	1559	27.80	11	63	9.23	95.74	30	245	40.19
2	1510	36.05	14	68	8.43	142.92	28	284	36.96
3	1409	41.74	20	82	9.18	190.52	82	364	54.28
4	1240	47.17	25	87	10.21	238.14	124	504	62.87
5	1097	52.94	29	89	9.63	301.18	153	510	75.34
6	847	56.96	34	84	9.35	327.48	194	476	55.08
7	480	62.06	40	84	7.98	345.99	241	437	38.90
8	282	65.77	43	91	8.24	370.32	274	427	31.28
9	85	66.55	50	89	7.33	369.11	308	422	24.53
10	37	68.41	55	81	5.64	382.30	336	430	18.98

sd, standard deviation.

matrix.

$$G = \begin{vmatrix} A\sigma^2_{1,1} & A\sigma_{1,2} & \cdots & A\sigma_{1,10} \\ A\sigma_{2,1} & A\sigma^2_{2,2} & \cdots & A\sigma_{2,10} \\ \vdots & \vdots & \ddots & \vdots \\ A\sigma_{10,1} & A\sigma_{10,2} & \cdots & A\sigma^2_{10,10} \end{vmatrix}$$

where:
A, additive genetic relationship;
σ^2_{ii}, genetic variance of trait *i;*
σ_{ij}, genetic covariance between traits *i* and *j;*
R, 10 by 10 block diagonal covariance matrices;

$$R = \begin{vmatrix} I\sigma^2_{1,1} & I\sigma_{1,2} & \cdots & I\sigma_{1,10} \\ I\sigma_{2,1} & I\sigma^2_{2,2} & \cdots & I\sigma_{2,10} \\ \vdots & \vdots & \ddots & \vdots \\ I\sigma_{10,1} & I\sigma_{10,2} & \cdots & I\sigma^2_{10,10} \end{vmatrix}$$

where:
I, = identity matrix;
σ^2_{ii}, variance for trait *i;*
σ_{ij}, covariance between traits *i* and *j* respectively for the random farm effect f and the random residual e.

Model 3 (M3) was a multiple trait individual animal model and it was similar to the previous one, but in this model:

y_i, was a vector of lamb weights with 14 age classes (from 2 to 15 months of age);

G, was a 14 by 14 additive genetic covariance matrix;

R, a 14 by 14 block diagonal covariance matrices: in fact, each weight was assigned to the nearest month of age of the lamb (Table 2).

Since the first age class was 2 months of age, and the last 15 months of age, the weights registered before 45 days or after 465 days were discarded, so that the records in M3 were 8124.

Model 4 (M4) was a Random Regression Model:

$$y = X ß + \sum_{m=0}^{q_ß} \beta\lambda_{tm} + \sum_{m=0}^{q_u} u\lambda_{tm} + \sum_{m=0}^{q_p} p\lambda_{tm} + \sum_{m=0}^{q_f} f\lambda_{tm} + e$$

where:
y, was a vector of lamb weights;
ß, was a vector of fixed effects including fixed quadratic regression for age, type of birth (single or twins) and weighing day (182 levels);
$\lambda = \phi$ t are the coefficients of the K random regression matrix of the Legendre polynomials ϕ of order *m* for age at recording t, standardized between -1 and +1;
u, was a vector of animal additive genetic effects;
p, was a vector of permanent environmental effects;
f, was a vector of farm effects;
e, was the vector of random residuals;
X, was the incidence matrix for fixed effects.
The variances for random effects were Var(u) = $A \otimes K_a$, Var(p) = $I \otimes K_p$, Var(f) = $I \otimes K_f$, Var(e) = $I\sigma_e^2$.

The order of the Legendre polynomials $q_ß = q_u = q_p = q_f$ was equal to 2: therefore, the lambs weighted less than four times were deleted, so that the dataset used in M4 contained 8081 weights.

In all models, the effect of the flock of origin was random, according with Oikawa and Sato (1997). The main statistical parameters and mixed model estimates were obtained by VCE (Groeneveld *et al.*, 2008). The impact of the models on the ranking of animals was estimated by the linear correlation between the traditional index based on ADGs and the EBVs from four models: 10 and 14 correlations were averaged for M2 and M3, while they were averaged throughout the whole age trajectory for M4; the effect on the approval of rams was assessed by Cohen's *k*, assuming that after each year the same proportion of lambs was approved according to ADG index or EBVs.

The relative quality of the statistical models has been assessed by means of the Akaike Information Criterion: since the models had different number of weights, the criterion was corrected for finite sample size (AICc) (Sugiura, 1978); due to the optimization strategy used by VCE, the AICc were calculated considering the animals as unrelated (Groeneveld *et al.*, 2008).

Results and discussion

The main statistics of the recorded weights and related ages during the test are in Table 1. The weights ranged from 28 kg (1st weighing day) to 68 kg (10th weighing day). Although the increase in weight, the standard deviation (sd) of weight reduced in time: because of this, the CV continuously decreased from 33.1% at 1st weighing day to 8.2% at 10th weighing day. The

Table 2. Statistics of weight and age, after assigning a record to the nearest month of age class (n=8124): dataset used in model M3.

Age class	N.	Weight, kg				Age, days			
		Mean	Min	Max	sd	Mean	Min	Max	sd
1 (60 days)	367	20.76	12	39	4.79	56.95	45	74	9.28
2 (90 days)	561	27.80	13	46	5.12	91.05	75	104	8.54
3 (120 days)	940	32.65	14	51	6.20	119.61	105	134	8.36
4 (150 days)	1076	36.86	19	63	6.78	149.61	135	164	8.42
5 (180 days)	951	41.20	22	66	6.98	178.58	165	194	8.47
6 (210 days)	765	45.06	24	68	7.58	208.34	195	224	8.42
7 (240 days)	665	48.56	27	71	7.77	238.54	225	254	8.39
8 (270 days)	507	52.57	31	71	8.00	269.16	255	284	8.76
9 (300 days)	423	53.83	31	82	8.62	298.60	285	314	8.70
10 (330 days)	563	57.23	34	78	8.53	331.35	315	344	7.89
11 (360 days)	678	61.11	39	89	8.47	358.13	345	374	8.29
12 (390 days)	466	65.50	37	91	9.12	387.94	375	404	8.05
13 (420 days)	117	65.79	39	87	10.88	416.12	405	434	8.53
14 (450 days)	45	56.63	47	74	6.97	452.27	435	464	10.22

sd, standard deviation.

ages showed a similar pattern, with CV reducing from 42 to 5% (not tabulated data); the trend was due to the culling of lighter lambs as the testing period goes on. In the first two weighing days, the minimum and maximum values were very similar, but there was an increase of more than 8 kg for the mean; also, the minimum age at the first two weighings did not change, whilst the mean age moved of 47 days. These facts confirm that there was a huge variation in the arrival of the lambs at the station and that some lamb missed the early weighing days. The weighing operation should take place monthly, but from 2nd to 3rd weighing, and from the 3rd to the 4th, the intervals were approximately of a month and a half, and there was an average interval of two months between 4th and 5th weighing. The maximum age (510 d) was registered at the 5th weighing then, after this point, the interval between weighing days decreased; in the last weighing days there was apparently no increase in age or weight statistics, a part for minimum weight. These facts show that in effect the lambs with the last records were only those who arrived later at the station.

Only 367 lambs out of 1609 (22.8%) arrived at the testing centre at two months of age, and the most frequent age at weighing was 5 months (n=1076). More than a half of the animals stayed at the station until one year of age, and after this age their number rapidly decreased: the mean weight stands at 66 kg from 390 to 420 days, and after this it decreases to 57 kg in the last class; these data show that only the lambs with lower weights stayed at the station after one year of age (Table 2). The 25 flocks at performance station were always connected genetically: in fact, 300 r_{bCG} out of 300 (*e.g.*, 25*24/2) were greater than 0; average r_{bCG} was 0.003 (range: 0.001-0.035), with a raising/trend of 0.0002/year; average r_{wCG} was 0.021. Genetic connections were present between 26.9% of farms (707 out of 2628), with a mean r_{bF} of 0.002 and a mean r_{wF} of 0.076. The increasing r_{bCG} shows the positive effect of the performance test in creating links in the Appenninica population; the genetic connectedness between contemporary groups of Appenninica sheep seems slightly below the level found in Italy for Sardinian sheep, a dairy breed (Salaris *et al.*, 2009). The M1 model is a repeatability model, although also the term repeatability is not appropriate: the trait is a live weight and a growing animal has just one live weight at each day. It is evident that M1 is not adequate, because the weights spanned over a wide period of lambs lifetime; from a biological point of view, probably the genes expressing in the weight of a young lamb are

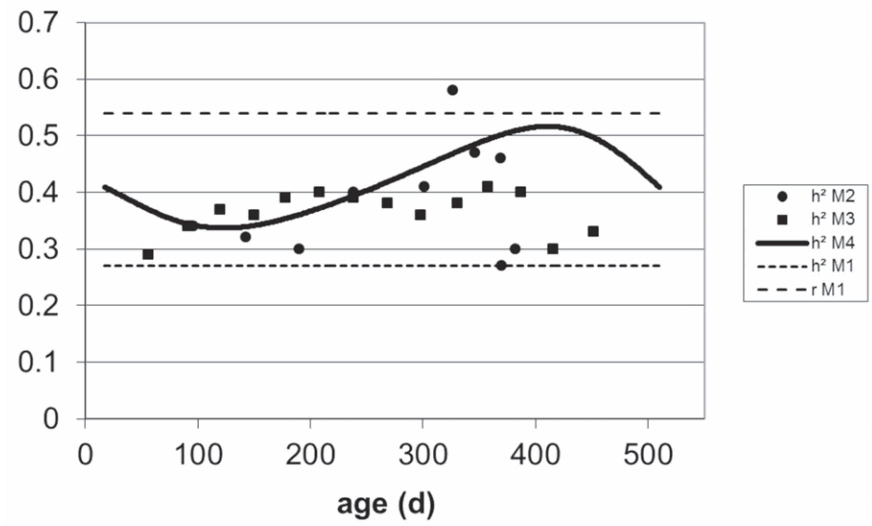

Figure 2. Plot of heritabilities estimated with M1, M2, M3 and M4 models.

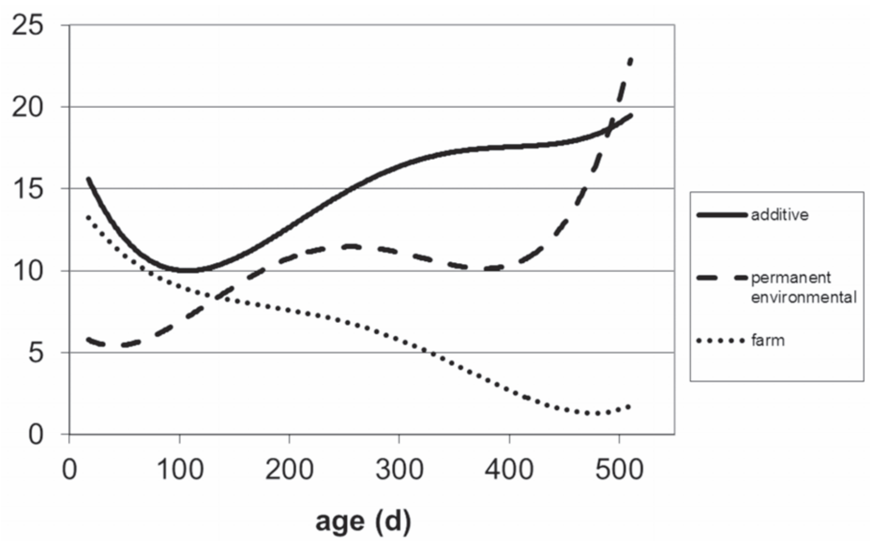

Figure 3. Plot of variance components estimated by random regression model M4.

Table 3. Heritability (h²) ±standard error of the weight at the subsequent weighing days during the performance test.

Weighing day	N.	Mean age, days	$h^2 \pm$ SE
1	1559	96	0.34±0.02
2	1510	143	0.33±0.01
3	1409	190	0.30±0.02
4	1240	238	0.40±0.01
5	1097	301	0.41±0.01
6	847	327	0.58±0.01
7	480	346	0.47±0.01
8	282	370	0.46±0.01
9	85	369	0.27±0.01
10	37	382	0.36±0.01

different from those expressing in the weight of a one-year-old ram. In the M1 model, the fixed effect *weighing* day had a great number of levels (182) and it was the interaction of the order of the weighing by the year of testing. This effect grouped together all lambs that shared a similar condition in the last period before the recording of their live weight; it could be very important because of the great variability in environmental conditions. We could define the trait in M1 as an *average live weight*: the estimates of genetic parameters for it could be an easy point of comparison with several estimates spanning along the same interval; this is the only practical use of M1 model, due to the weakness previously mentioned. The heritability and repeatability *(mean±se) of the* average live weight, estimated by M1, were 0.27±0.04 and 0.54±0.08 respectively.

The heritabilities of lambs weight recorded at the different weighing days estimated by M2 (Table 3) show similar estimates for the first three records, where the values ranged from 0.30 to 0.34; in the 4th and 5th records, the values raised to 0.40 and 0.41, and a further increase is found in the next three weighings. In the last two weighings, the estimates fall down, especially in 9th one. It is evident that, because of the variability in the age of lambs at the entrance and in the spacing of weighing operations, lambs of the same age could be in different order of record, and *vice versa* in the same order there could be lambs of different ages. This fact is a clear drawback of M2, whose strength is that the considered traits probably relate to the time in the station better than to the age of the lamb; this point is important because of the inclusion of the farm of origin in the models. The genetic correlations (data not shown) between two consecutive weighings estimated by M2 model ranged between 0.71±0.02 (1st *vs* 2nd weighing) and 0.98±0.01 (8th *vs* 9th weighing), while the overall minimum was 0.31±0.04 between 1st and 9th weighing.

The heritabilities of weights at the different age classes (Table 4), estimated by means of M3, show a narrower variability than M2 estimates: in fact, they range between 0.29 (1st class, 60 d) and 0.41 (11th class, 1 year). The reduction in the number of observations in each class explains the larger standard error (SE) of these estimates: in fact, 10 weighing days spanned into 14 monthly classes; furthermore, when two weights of the same lamb converged in the same age class, only the closer to the class central value was useful. The minimum genetic correlations (data not shown) between two consecutive age classes was between 13th and 14th class (0.04±0.08): this is a further evidence of the already stated problems that affect the last recordings. A part from the 1st, 13th and 14th age classes, which showed a reduced number of lambs, the genetic correlations ranged between 0.77±0.05 (2nd *vs* 3rd class) and 0.97±0.02 (9th *vs* 10th class); the overall minimum was 0.10±0.06 between 2nd and 12th class. The estimates of live weight heritability by random regressions (M4) ranged between 0.34 at 123 d of age and 0.52 at 411 d. The plot of M4 estimates by age (Figure 2) shows a rather sinusoidal pattern: the increase of heritability by age between 123 and 411 d is consistent; however, two decreasing periods are shown at the extremes. The plot of additive, permanent environmental and farm variance by age (Figure 3) shows that the effect of the origin farm regularly decreased: this fact was expected, because with the aging of lambs also the period since it left the farm increases. In the first days, the additive variance decreased too, and this causes the initial decrease of heritability: since additive variance always increased after 108 d, the final decrease in heritability was due to the permanent environmental component, which showed a huge raise after 377 d.

Table 4. Heritability (h^2)±standard error of the weights assigned to the nearest age class.

Age class	N.	Mean age, days	h^2 ± SE
1 (60 days)	367	56	0.29 ± 0.06
2 (90 days)	561	91	0.34 ± 0.05
3 (120 days)	940	120	0.37 ± 0.04
4 (150 days)	1076	150	0.36 ± 0.03
5 (180 days)	951	178	0.39 ± 0.02
6 (210 days)	765	208	0.40 ± 0.03
7 (240 days)	665	238	0.39 ± 0.03
8 (270 days)	507	269	0.38 ± 0.03
9 (300 days)	423	298	0.36 ± 0.04
10 (330 days)	563	331	0.38 ± 0.03
11 (360 days)	678	358	0.41 ± 0.03
12 (390 days)	466	387	0.40 ± 0.04
13 (420 days)	117	416	0.30 ± 0.05
14 (450 days)	45	452	0.33 ± 0.04

The average linear correlation between the traditional index based on ADGs and the EBVs from the four models ranged from 0.25 for M3 to 0.31 for M2; M1 and M4 showed the same intermediate value (0.26). The low correlations between the phenotypic index and the EBVs had a great impact on the approval of rams, evaluated by Cohen's *k*: in fact, this coefficient showed poor concordance for M1 to M3 (*k*= 0.28, 0.26 and 0.24 respectively), with a minimum for M4 (*k*=0.12). The lowest AICc was showed by M4, followed by M2, M1 and finally M3 in this order (M1=-11158.296961; M2=-37623.377189; M3=-23903.799425; M4=-63279.587526): although the AICc were calculated considering the animals as unrelated, and the small differences in the datasets, the values indicate that a change in this adequacy order is very unlikely (Burnham and Anderson, 2002). The heritability and repeatability values estimated in the general weight trait were close to 0.30 and 0.50 respectively; these values are similar to that computed by others in different breeds. Borg *et al.* (2009) in 12154 Targhee lambs estimated h^2 close to 0.20-0.30 for the weight at ages between birth and 18 months. Heritability coefficients for the weights in the same range of age were estimates also by Eskandarinisab *et al.* (2010) in a population of 1478 Afshari lambs. Also Kariuki *et al.* (2009) in Dorper sheep found h^2 ranging from 0.14 to 0.36 in the weight at birth up to one year. About the heritabilities estimated at the different weighing days, the lower values observed in the last records could be due to the reduction of the number of animals and the distribution of their ages commented above. This is a further evidence that mainly lambs that arrived too late and/or had problems during the test are weighted in the last days. The M2 showed a large variability of the estimates: as a consequence of this, the overall index of a ram from M2 could reflect the random variability of the weighing days in the different years of testing.

Previous estimates of the heritability of live weight at different ages in Appenninica breed were lower, ranging from 0.15 to 0.34 (Sarti *et al.*, 2001): in part, this can be because the estimates referred to a commercial stock. The estimates computed here by random regression are higher than values reported by other authors. Safary and Fogarty (2003) reported h^2 coefficients equal to 0.25, 0.19 in Polled Dorset and 0.25 in Belgian Texel respectively for the weights at 110 d, 220 d and 350 d of age. Atkins *et al.*, (1991) estimated heritabilities from 0.21 and 0.31 on 20159 Australian Poll Dorset lambs aged from 4 to 16 months. The sinusoidal pattern and the increase of heritability with age between 123 and 411 d are consistent with literature (Safary and Fogarty, 2003).

Concerning the reduced heritabilities at the beginning and at the end of the plot in Figure 2, it must be considered that the weights at these periods do have a very low number of records, and that they refer to the period that had more variability between years. It has been pointed out that the extremes of the time scale can show artifacts in RR models based on Legendre polynomials if few observations are present (Misztal *et al.*, 2000): in these situations, RR models using linear splines seem to perform better (Misztal, 2006). The faster decrease after the maximum is in contrast with Fischer *et al.* (2004), which on a population of 5400 Poll Dorset lambs, found an increase after 450 d. The estimates at 3 and 8 months of age are very similar to those from M2 and M3 models: therefore, the evaluation model could have a lower effect in the estimates of breeding values at these ages. After the admitting period is closed, it could be useful to calculate a mean age of the lambs, and to do any effort to perform two weighing days around the mean ages of 3 and 8 months. This is because the live weight at 90 days is very important in the Italian market, and the EEC regulations (N.2137/92) consider the lambs around this age in a special class called *heavy lamb.*

Conclusions

The records of Appenninica rams in performance test station showed a great variability in age at weighing and number of records by year. If the weights are only the mean to calculate an average daily gain, this inconvenience vanishes; to get genetic estimates of weights, the heterogeneity of the dataset requires many corrections: this was strategy in M3. The random regression model was a better way to correct the effect of different ages at the weighing date, but switching to any model based on EBVs will produce great differences on the approval. Since different models showed very similar estimates of weights at 3 and 8 months of ages, and in the Italian market light lambs receive a higher price, the station test must be programmed so that the weights at these two ages are always collected.

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