

Inbreeding depression in the Lizard canary breed estimated by pedigree analysis

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ABSTRACT: The influence of inbreeding depression on phenotypic traits of the Lizard canary from an Italian breeder was evaluated. The following traits were studied: birds' life span, number of surviving offspring, and morphological traits (type of plumage, spangles, feather quality, breast, cap, ground colour, wings and tail, eyelashes, covert feathers, beak, legs and feet, habits, and size). The effects of inbreeding on genetic diseases and on the health of the breed were also considered. The inbreeding coefficient of each bird was computed by genealogical data. The distribution of inbreeding in the whole population was analyzed and eleven different inbreeding level classes were considered. Birds were also divided into healthy and unhealthy animals (animals with genetic abnormalities such as blindness, splay legs and cataracts, or genetic predispositions, such as feather cysts (lumps), or animals with slow growth and/or a slender structure). Despite the high levels of inbreeding in the population, the results showed that 80.47% of the birds were healthy and no significant differences were observed between healthy and unhealthy animals in terms of the degree of inbreeding. Evidence of inbreeding depression was observed in the number of surviving offspring and the life span, whereas phenotypic characters did not show any evidence of inbreeding depression.

Keywords: genetic disease; life span; number of surviving offspring; phenotypical traits

INTRODUCTION

Inbreeding occurs when pair members share common ancestors or when they are more closely related than two randomly chosen individuals from the population. Inbreeding produces progeny with reduced levels of individual heterozygosity, increasing the risk of expressing recessive deleterious alleles. Mating among relatives generally changes genotype frequencies in populations and can result in a decline in mean phenotype and fitness, a phenomenon known as inbreeding depression, which has been described as a potential animal welfare problem. Most studies of inbreeding depression measure only one or a few components of reproductive fitness. However, since all traits have the potential to accumulate deleterious recessive alleles as a result of mutations, all components of reproductive fitness are expected to be subject to inbreeding depression (Ralls et al. 2013). In animals, this includes offspring survival and

other parameters. Inbreeding effects have been extensively studied in wild populations (Keller and Waller 2002; Brekke et al. 2010; Brzeski et al. 2014). A review of the literature on inbreeding effects in wild vertebrates and plants found that 90% of 157 datasets showed inbreeding depression. This thus indicated that different species, such as mammals, birds, fishes, reptiles, snails, insects and many species of plants, frequently exhibit moderate to high levels of inbreeding depression under natural conditions (Crnokrak and Roff 1999).

Many studies are also available for dogs (Cecchi et al. 2015) and for livestock such as sheep (Mandal et al. 2005; Hossein-Zadeh 2012), goat (Khan et al. 2007), horse (Curik et al. 2003), pig (Silio et al. 2012), cattle (Gonzalez-Recio et al. 2007), buffaloes (Malhado et al. 2013), and hens (Niknafs et al. 2013).

Inbreeding depression has been investigated through a large variety of models and hypotheses according to the type of available data (Leroy 2014). Inbreeding depression can be estimated as a linear

regression coefficient between a phenotypic value and inbreeding coefficient computed by genealogical data. Therefore, whatever trait or population is taken into account, it is possible to consider a scaled estimation by dividing the regression coefficient by the mean of the phenotypic trait (Flock et al. 1991; DeRose and Roff 1999; Gomez-Raya et al. 2009) or by the phenotypic standard deviation (Leroy 2014). Another measure of inbreeding depression is the coefficient of inbreeding depression δ (Lande and Schemske 1985), which is calculated as the proportional decrement in the expected fitness of inbred animals compared to the expected fitness of non-inbred animals. Other authors have used individual inbreeding rate ΔF , developed by Gutierrez et al. (2009), instead of the pedigree coefficient.

When based on genomic information, runs of homozygosity (ROH) is considered the best approach to estimate inbreeding, as it distinguishes between identity by descent and identity by state (Keller et al. 2011). In a previous paper (Cecchi et al. 2014), we analyzed the genealogical information of a Lizard canary population bred on a single Italian farm in order to ascertain the genetic variability of the population. All the results showed that inbreeding was very high and that the loss of genetic variability was rather high. In fact, the average value of inbreeding (F) was 14.25 and the trend in inbreeding was estimated to be 6.71% per generation, which was above the acceptable range of 0.5–1% recommended by the FAO (1998) guidelines for livestock populations.

The aim of this study was to extend our previous analysis on the same farm by evaluating the effect of inbreeding depression. This was estimated using the inbreeding coefficient (F) obtained from genealogical data on the canary life span, number of surviving offspring, and various phenotypic traits as well as the health and genetic abnormalities of the canaries.

MATERIAL AND METHODS

Animals and data. The research was carried out on a Lizard canary farm in Italy from 2000 to 2012. The canaries were housed in a building (6 × 5 m) with two windows and a glass door, and supplied with a forced-ventilation system plus natural and artificial lighting. During the period of reproductive inactivity, canaries were reared in an aviary (1 m in length; 6–9 canaries/aviary); males and females

were kept in separate aviaries before the beginning of the reproductive season. The onset of the reproduction was at about one year of age. The Lizard breeder pairs were chosen on the basis of phenotypic characteristics (spangles and shape/size, rowings, ground colour, beak, and legs). Each couple of canaries was reared in a cage (60 cm in length) from March to June. The partners of unfertile pairs were replaced to obtain fertile pairs. Each close-knit couple lived together throughout the year with the same probability of reproducing and having offspring.

Genealogical and health status data of 471 birds (191 males, 199 females, and 81 not sexed), born between 2000 and 2011, were monitored.

For each male and female various phenotypic traits were considered with the scoring performed by a judge from the Lizard Canary Association (L.C.A.) or the World Ornithological Confederation (C.O.M.). The description and the scale of points for each trait are summarized below:

Spangles: the net and completeness of the design were evaluated to estimate the drawing back. The design starts at the posterior limit of the cap and ends by covering the wings, and the rows proceed in a straight line and are parallel to each other. In the Lizard canary without a cap the spangles must also cover the head (maximum score = 25 points);

Feather quality: the quality of plumage was evaluated considering the following characteristics: similar to velvet; flexible, compact, and brushed to give a luminous effect. Good quality plumage highlights the design (maximum score = 15 points);

Breast (chest design): the following parameters were considered in evaluating the chest design: sickle-shaped, sharp, distinct, perfectly aligned flakes. The chest begins under the beak and reaches as far as the tail (maximum score = 10 points);

Cap: the following characteristics were considered in evaluating the cap: the dimension of the head must be fairly large, round, and full on the top. The cap extends from the base of the upper mandible to the base of the skull and is oval in shape with clearly defined edges. The cap was classified as follows: clear cap (perfectly clear), broken cap (the light area of the cap is more or less broken by dark feathers), and no cap (without crown, replaced by dark feathers) (maximum score = 10 points);

Ground colour: the colour was evaluated in terms of depth and evenness: it must be golden, deep, evenly distributed, and with no infiltration of another shade (maximum score = 10 points);

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Wings and tail: evaluated in terms of neatness and dark colour: both traits must have as dark a colour as possible (maximum score = 10 points);

Eyelashes: evaluated for regularity and clarity: a line of dark feathers passing above the eye of the bird and giving a good finish to the cap (maximum score = 5 points);

Covert feathers: assessed in terms of being sharp, distinct, and aligned to form a dark or almost black drawing (maximum score = 5 points);

Beak, legs, and feet: must be well oxidized (maximum score = 5 points);

Habits and size: the bird must show a perfect condition and must be calm. With regard to size, the C.O.M. requires 12.5 cm (maximum score = 5 points), while the English standard of the L.C.A. requires the length not to exceed 13.335 cm but without providing specific scores.

Moreover, the type of plumage was considered – evaluated according to gold or silver colour (maximum score = 90 points).

Statistical analysis. The number of inbred birds and the inbreeding coefficient of each bird were obtained using CFC software (Sargolzaei et al. 2006). The distribution of inbreeding in the whole population was analyzed. Eleven different classes of inbreeding were identified by the software: class 1 including non-inbred animals ($F = 0$); all the other ten classes including inbred animals (class 2: $0 < F \leq 0.05$; class 3: $0.05 < F \leq 0.10$; class 4: $0.10 < F \leq 0.15$; class 5: $0.15 < F \leq 0.20$; class 6: $0.20 < F \leq 0.25$; class 7: $0.25 < F \leq 0.30$; class 8: $0.30 < F \leq 0.35$; class 9: $0.35 < F \leq 0.40$; class 10: $0.40 < F \leq 0.45$; class 11: $0.45 < F \leq 0.50$).

Concerning the health data, all 471 animals were divided into two classes: (1) Healthy animals, (2) Unhealthy animals (animals with genetic abnormalities such as blindness, splay legs and cataracts, or genetic predisposition such as feather cyst – lumps, or animals with slow growth and/or slender structure).

Life span data and the number of surviving offspring were calculated for 104 dead animals (50 males and 54 females).

To assess the effects of inbreeding on the health of the Lizard canaries, the distribution of animals belonging to different classes of inbreeding in the two health classes was considered.

All the differences between sexes and inbreeding classes or between health classes on phenotypic traits and on the life span of the birds were tested using the following model:

$$Y_{ijkl} = \mu + S_i + HF_j + B_k + \varepsilon_{ijkl}$$

where:

Y_{ijkl} = parameters considered

μ = overall mean

S_i = fixed effect of the i^{th} sex ($i = 1, 2$)

HF_j = fixed effect of the j^{th} health class ($j = 1, 2$) or fixed effect of the j^{th} inbreeding class ($j = 1, \dots, 11$)

B_k = fixed effect of the k^{th} year of birth ($k = 2000, \dots, 2011$)

ε_{ijkl} = residual error

All analyses regarding the number of surviving offspring were performed by introducing the covariate for the life span of the birds in the model.

Estimation of inbreeding depression. A linear regression of each inbreeding coefficient trait was added to the model (excluding the fixed effect of the F class) to estimate the inbreeding depression. Solutions were given per 1% increase of inbreeding.

Furthermore, for each trait, we only considered the not inbred canaries ($F = 0$: 30 dead birds in terms of life span and the number of surviving offspring; 162 birds for morphological traits) and the canaries with $F = 0.25$ (19 dead birds for life span and the number of surviving offspring; 45 birds for morphological traits) and we used the coefficient of inbreeding depression δ (Lande and Schemske 1985) that is in this case the decline of the average value of a trait due to an inbreeding value of 0.25:

$$\delta = 1 - (X_1/X_0) = (X_0 - X_1)/X_0$$

where:

X_1 = inbred ($F = 0.25$) trait mean value

X_0 = outbred trait mean value

All experimental data obtained were analyzed using the SAS (Statistical Analysis System, Version 5.0, 2002) software.

RESULTS AND DISCUSSION

Results of this study showed that 379 of the considered birds (80.47%) were healthy, and that 141 of these animals (37.20%) were not inbred, while 69 birds (18.20%) had a higher inbreeding coefficient than 0.25 (Figure 1). There were 45 birds with $F = 0.25$ (19 dead animals and 26 live animals).

No significant differences in the average value of the inbreeding coefficient (0.12 ± 0.007 for healthy birds and 0.14 ± 0.056 for unhealthy birds) and

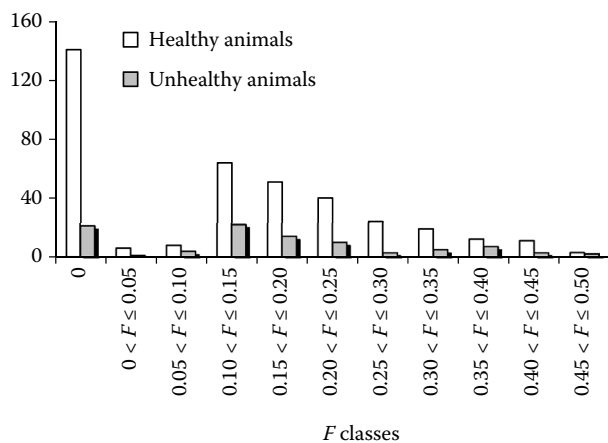


Figure 1. Number of healthy and unhealthy canaries for each class of inbreeding

in morphological traits between the two health status classes were observed. As reported by Jansson and Laikre (2013) in 26 different dog breeds, the inbreeding did not explain the differences in health problems within the breeds.

Concerning the different classes of inbreeding, no differences were found in terms of morphological traits, however differences were highlighted in the number of surviving offspring ($P \leq 0.01$) and life span ($P \leq 0.05$) (data not shown).

Table 1 reports on the differences between males and females. Significant differences were found regarding ground colour ($P \leq 0.001$), cap ($P \leq 0.05$), and covert feathers ($P \leq 0.01$). No significant differences between males and females were found in the average life span and the average number of surviving offspring. The average inbreeding coefficient was 0.12 ± 0.098 in males, and 0.15 ± 0.085 in females (data not shown).

Table 2 shows the regression coefficients of inbreeding traits of birds for a change of 1% in inbreeding. The regression coefficients of the number of surviving offspring and of birds' life span on inbreeding for 1% change in inbreeding were significantly negative (-0.101 , $P \leq 0.01$ and -0.067 , $P \leq 0.05$, respectively), while the regression coefficients of phenotypic trait scores for inbreeding were not significant. As is well known, the inbreeding depression is mainly manifested in the traits closely related to fitness such as viability, mortality, and reproduction. However it is also important to know its effects on morphological data, which have a major impact on the choices made by farmers and amateur breeders.

Table 1. Differences in traits between males and females

Traits	Males	Females
	$n = 50$	$n = 54$
Life span (years)	4.55 ± 0.711	4.45 ± 0.645
Surviving offspring (n)	9.17 ± 3.833	6.60 ± 2.939
	$n = 191$	$n = 199$
Type of plumage (score)	86.61 ± 9.800	87.85 ± 7.170
Spangles (score)	20.73 ± 1.287	21.56 ± 7.916
Feather quality (score)	12.69 ± 0.642	12.75 ± 0.523
Breast (score)	9.35 ± 0.805	8.72 ± 0.703
Cap (score)	8.63 ± 0.557^b	8.77 ± 0.567^a
Ground colour (score)	9.10 ± 0.574^A	8.75 ± 0.581^B
Wings and tail (score)	8.89 ± 0.691	8.88 ± 0.647
Eyelashes (score)	5.00 ± 0.000	5.00 ± 0.000
Covert feathers (score)	4.55 ± 0.570^B	4.71 ± 0.528^A
Beak, legs, and feet (score)	4.92 ± 0.264	4.90 ± 0.342
Habits and size (score)	5.00 ± 0.000	5.00 ± 0.000

^{A,B} $P < 0.01$, ^{a,b} $P < 0.05$

Swinerton et al. (2004) reported that inbreeding affected juvenile and adult survival of the endangered pink pigeon *Columba mayeri*, however the effects were the strongest in highly inbred birds ($F \geq 0.25$). The regression coefficients of phenotypic trait scores on inbreeding of birds were estimated to be negative but not significant for many scores, and positive for the scores regarding chest design, cap, wings and tail, and covert feathers.

Table 2. Regression coefficients (b) of traits on inbreeding of birds for a change of 1% in inbreeding

Traits	b	P
Life span	-0.067	*
Surviving offspring n	-0.101	**
Type of plumage	-0.168	ns
Spangles	-0.002	ns
Feather quality	-0.004	ns
Breast	0.003	ns
Cap	0.006	ns
Ground colour	-0.003	ns
Wings and tail	0.002	ns
Eyelashes	–	
Covert feathers	0.003	ns
Beak, legs, and feet	-0.004	ns
Habits and size	–	

* $P < 0.05$, ** $P < 0.01$, ns = not significant

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Table 3. Traits, outbred trait mean values (X_0), inbred ($F = 0.25$) trait mean values (X_1), sample sizes, and calculated levels of inbreeding depression

Traits	X_0	Outbred n	X_1	Inbred n	δ^1
Life span (years)	5.33	30	4.32	19	0.189
Surviving offspring n	11.97	30	7.071	19	0.409
Type of plumage (score)	87.96	162	86.97	45	0.011
Spangles (score)	21.27	162	20.82	45	0.021
Feather quality (score)	12.87	162	12.77	45	0.008
Breast (score)	8.39	162	8.60	45	-0.025
Cap (score)	8.61	162	8.85	45	-0.028
Ground colour (score)	8.92	162	8.84	45	0.009
Wings and tail (score)	8.92	162	9.02	45	-0.010
Eyelashes (score)	5.00	162	5.00	45	0.000
Covert feathers (score)	4.50	162	4.53	45	-0.007
Beak, legs, and feet (score)	5.00	162	4.92	45	0.016
Habits and size (score)	5.00	162	5.00	45	0.000

¹coefficient of inbreeding depression $\delta = 1 - (\text{inbred mean value}/\text{outbred mean value})$

The inbreeding depression (Table 3) calculated using Lande and Schamske's formula (1985) confirmed the previous results. For the estimate of δ , the inbreeding depression values were 0.409 ($X_0 = 11.97$, $X_1 = 7.071$) for the number of surviving offspring and 0.189 ($X_0 = 5.33$, $X_1 = 4.32$) for life span (Table 3). This method showed contrasting values compared to the regression method because it considered the difference in each trait between non-inbred ($F = 0$) and inbred animals ($F = 0.25$) divided by the value of non-inbred animals. In this case one positive value showed a reduction in the performance of inbred animals compared to non-inbred animals (which is the superiority of non-inbred animals). Negative values pointed to the positive effects of inbreeding.

As is well known, the same trait in different breeds and populations varies in response to inbreeding: some populations show a very pronounced effect of a trait in response to increased inbreeding, whereas others may not demonstrate much of the effect. Several studies on livestock species have shown the heterogeneity of inbreeding depression with neutral or negative or positive effects on different traits (Leroy 2014). As reported by Barczak et al. (2009), in a given population "bad" and "good" inbreeding effects are mixed. It is also important to emphasize that the degree of inbreeding depression in a population depends on the extent of inbreeding, original frequency of deleterious recessive alleles, environment, and that

the inbreeding depression may be greater under more stressful conditions (Marr et al. 2006).

To our knowledge, there are no published papers regarding the effects of inbreeding on canary traits. However, the inbreeding depression values observed in the present study were similar to findings reported by Crnokrak and Roff (1999) in terms of brood size in *Aphelocoma ultramarine*, but higher than those observed for other traits (such as clutch size, nest success, number of eggs hatched, percentage of eggs fledged, number of young surviving or fledged) analyzed by the same authors in other birds (*Accipiter cooperi*, *Aphelocoma ultramarine*, *Geospiza fortis*).

In our study the inbreeding depression value detected for the number of surviving offspring ($\delta = 0.403$) was sufficiently high (> 0.33) to be considered as biologically important (Frankham 1995). This finding highlights that it is necessary to control inbreeding in the population, which can be achieved by optimizing the contribution of the parents in minimizing the average kinship. Exploiting computerized files and statistical software to calculate the relationship between the two animals of the pair can certainly support the farm management.

Outbreeding is a potentially useful tool, especially to introduce diversity. Indeed, the inbreeding depression can be completely reversed by outcrossing an inbred population to another unrelated population, either an outbred population or another inbred population. Crossing two highly inbred,

but unrelated, populations results in an outbred population with a high level of heterozygosity and little inbreeding depression. This is because the high heterozygosity effectively masks the deleterious alleles that were expressed in the inbred populations. This effect is known as “hybrid vigour”. Partial recovery can be achieved by introducing unrelated individuals into an inbred population.

CONCLUSION

This research analyzed for the first time the effects of inbreeding on health and on various phenotypic characteristics of a population of canaries. Both methods used to estimate the inbreeding depression showed the negative effects of inbreeding on the number of surviving offspring and on the canaries’ lifespan, but had no effects on morphological traits. In addition, the present study revealed that, despite the high levels of inbreeding highlighted in the population, more than 80% of the animals were healthy.

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