Arch. Tierz., Dummerstorf **46** (2003) 3, 277-284

[1]Department of Sheep and Goat Breeding, August Cieszkowski Agricultural University of Poznań, Poland
[2]Department of Human Biological Development, Institute of Anthropology, Adam Mickiewicz University, Poland

MARCIN TADEUSZ GÓRECKI[1] and KRZYSZTOF KOŚCIŃSKI[2]

Offspring sex ratio in domestic goat (*Capra hircus*)

Abstract

The *Capra* genus is sexually dimorphic, males are substantially bigger than females, they fight for mating privileges and sometimes even form harems. Thus *Capra* genus meets the assumptions of the Trivers-Willard hypothesis. However, in case of the domestic goat *Capra hircus* their reproduction is man-managed. We assessed whether maternal hornedness, maternal and paternal breed and age, maternal birth year, litter size, previous year offspring sex, and litter birth year influenced offspring sex ratio in the domestic goat. We examined 268 litters born in the years 1997-2002 at the Experimental Farm in Złotniki. The statistic methods used were logistic regression and Spearman rank correlation. The offspring sex ratio in the herd differed significantly from unity: 55.8% kids were females, $p < 0.01$. The factors that significantly influenced offspring sex ratio were maternal hornedness and maternal birth year. Horned dams (occupying high positions in the social hierarchy) produced fewer daughters (52.2% of offspring) than hornless nannies (62.2%). The fact that dams born later produce more daughters can be connected with their origin from different farms and worse environmental conditions in Złotniki in the consecutive years (because of the Experimental Farm financial problems). Moreover, Spearman rank correlation between sex ratio in the first and in the second litter was marginally significant and negative ($R = -0.25$, $p = 0.061$).

Key Words: goat, offspring sex ratio, hornedness, social hierarchy

Zusammenfassung

Titel der Arbeit**: Das Geschlechtsverhältnis der Nachkommen bei der Hausziege** ***(Capra hircus)***
Die Gattung Capra ist durch geschlechtlichen Dimorphismus gekennzeichnet. Die männlichen Tiere sind deutlich größer als die weiblichen, sie kämpfen um die Möglichkeit der Kopulation und zeitweilig bilden sie Harems. Demnach erfüllt die Gattung Capra die Voraussetzung der Trivers-Willard-Hypothese. Bei der Hausziege *Capra hircus* wird die Fortpflanzung jedoch vom Menschen gesteuert. In vorliegender Arbeit wird untersucht, ob die Hornigkeit des Muttertieres, Rasse und Alter der Eltern, Geburtsjahr der Mutter, Größe des Wurfes, Geschlecht der Nachkommen im Vorjahr oder das Geburtsjahr des Wurfes das Geschlechtsverhältnis der Nachkommen bei der Hausziege beeinflusst. In die Untersuchung wurden 268 Würfe unterschiedlicher genetischer Gruppen, die in den Jahren 1997 bis 2002 geboren wurden, einbezogen und die Daten biostatistisch ausgewertet. Das Geschlechterverhältnis der geborenen Lämmer war ungleich und die männlichen Nachkommen erreichten einen Anteil von 55,8 % (p <0,01). Den relativ größten Einfluss auf das Geschlechterverhältnis übten die Hornigkeit und das Geburtsjahr der Mütter aus. Hornige Mütter, die einen höheren Rang in der sozialen Hierarchie haben, gebaren weniger Töchter (52,2 % der Nachkommen) als die hornlosen Mütter (62,2 %). Dass die später geborenen Mütter mehr Töchter gebaren, wird auf die Herkunft aus unterschiedlichen landwirtschaftlichen Betrieben sowie auf sich verschlechternde Umweltbedingungen des Untersuchungsbetriebes zurückgeführt. Die Rangkorrelation zwischen dem ersten und dem zweiten Wurf war gering negativ (R=-0,25; p=0,061). Die weiteren Einflussgrößen werden diskutiert.

Schlüsselwörter: Ziege, Geschlechtsverhältnis der Nachkommen, Hornigkeit, soziale Hierarchie

Introduction

There are many factors influencing offspring sex ratio in mammals: parental age (JACOBSEN et al., 1999; NICOLICH et al., 2000; CÔTÉ and FESTA-BIANCHET, 2001; LANDETE-CASTILEJOS et al., 2001), maternal body condition (KOJOLA, 1997; CAMERON et al., 1999; HEWISON et al., 1999; KOHLMANN, 1999; WAUTERS et al., 1995; LANDETE-CASTILEJOS, 2001), maternal social rank (CASINELLO and GOMENDIO, 1996; KOJOLA, 1997), the season of the mother's birth (NONAKA et al., 1999), maternal nutritional condition (MONARD et al., 1997; KRUUK et al., 1999; MYSTERUD et al., 2000; ENRIGHT et al. 2001), maternal emotional stress (BAKKEN, 1998), previous year offspring sex (MONARD et al., 1997), the season of offspring birth (MILLESI et al., 1999; NONAKA et al., 1999), litter size (JACOBSEN et al., 1999), coat colour (TRUT, 1996) and population history (GRAFFELMAN and HOEKSTRA, 2000; NUNN and PEREIRA, 2000). The factors mentioned above can also interact with each other.

Two main adaptive explanations for offspring sex ratio variations have been proposed. According with TRIVERS and WILLARD (1973), if one sex receives more parental investment, parents in good condition will bias their investment toward the sex with the greater rates of reproduction returns. The theory deals especially with polygynous species. So mothers being in good condition (which can be dependent on their high social rank) should invest more resources in sons and mothers in poor condition ought to bias their investment toward daughters.

An alternative hypothesis is the local resource competition model (CLARK, 1978; modified by SILK, 1983). The model postulates that high-quality females should produce more offspring of the philopatric sex, because they will 'inherit' maternal social rank and home range. In mammals dispersing sex are usually males so mothers in good condition should bias their investment toward daughters and poor-quality mothers – toward sons.

The *Capra* genus meets the assumptions of the Trivers-Willard hypothesis. Males are substantially bigger than females, they compete with one another for mating privileges and sometimes even form harems (NOWAK, 1999). In case of the domestic goat *Capra hircus*, however, reproduction is managed by a breeder. We assessed whether maternal hornedness, maternal and paternal breed and age, maternal birth year, litter size, previous year offspring sex and litter birth year influenced offspring sex ratio in the domestic goat.

Material and method

We examined 268 litters totalling 527 kids (Table 1) born in the years 1997-2002 at the August Cieszkowski Agricultural University of Poznań Experimental Farm in Złotniki, Poland. Kids descended from 94 mothers (age ranged from 1 to 10 years, with the mean, for all litters, of 2.84 and the standard deviation of 1.77) and 9 fathers (age from 1 to 5 years, with the mean of 2.63 and the standard deviation of 0.88). These goats were Polish White Improved (Saanen type), Boers (billies only) and crosses of these two breeds (dams only). They came from different herds. We examined 150 litters born by 52 hornless dams, 100 litters born by 29 horned ones and 18 litters born by 13 dams with unknown hornedness. The number of kids in a litter ranged from 1 to 5 (Table 1). Standard deviations of sex ratios in the litters were in good accordance with the theoretically expected from the assumption of the binomial distribution of the trait (Table 1), so one can suspect there is no correlation between the sex of kids in a litter.

Sex is a dichotomous trait. Daughters were coded as 1 (success) and sons as 0 (failure). So sex ratio values are within the 0 to 1 range. Thus, we used logistic regression to search for the determinants of the sex ratio. The logistic regression equation can be expressed as follows:

$\ln(y/(1-y)) = b_0 + b_1 \times x_1 + ... + b_n \times x_n$

where $x_1, ..., x_n$ are independent variables, $b_0, ..., b_n$ are regression coefficients and y is the predicted sex ratio (the probability of the birth of a daughter). Expression $\ln(y/(1-y))$ is a logit transformation and is often written as logit(y). When the influence of x_i on y appears significant one can calculate the so-called odds ratio for two levels of x_i. The odds ratio shows how many times the odds to be a daughter, when x_i is on one level, are bigger than when x_i is on the other level.

Table 1
Litter size and sex ratio - descriptive statistics

Litter size	Number of litters	Number of kids	Proportion of daughters		
			Mean	Standard deviation	
				Observed	Expected
1	68 (25.37%)	68 (12.90%)	0.603	0.493	0.489
2	149 (55.60%)	298 (56.55%)	0.554	0.364	0.352
3	45 (16.79%)	135 (25.62%)	0.563	0.292	0.286
4	4 (1.49%)	16 (3.04%)	0.438	0.125	0.248
5	2 (0.75%)	10 (1.90%)	0.500	0.141	0.224
Total	268	527	0.558	0.386	

Eight traits were tested for influencing the sex ratio: maternal traits, i.e. hornedness, the year of birth, breed and age; paternal traits, i.e. breed and age; and litter traits, i.e. the year of birth and the number of kids.

Dependencies between sex ratios in consecutive litters (the first with the second, the first with the third, *etc.*) and between the sex ratio and the maternal year of birth were checked with the Spearman ranks correlation.

All calculations were conducted with StatSoft Statistica 2000.

Results

There were 294 females and 233 males among kids, which produced the proportion of daughters amounting to 0.558 (significantly different from 0.5, $p = 0.0079$).

Table 2
Determinants of offspring sex ratio (proportion of females) – results of logistic regression

	Estimates	Standard error	*p* level
Model with all traits:			
Constant	-267.529	0.582	0.616
Maternal hornedness	-0.575	0.215	0.008
Breed of mother	0.298	0.227	0.189
Maternal year of birth	0.024	2.881	0.993
Age of mother	-0.102	2.882	0.972
Breed of father	0.349	0.231	0.132
Age of father	-0.007	0.123	0.957
Offspring year of birth	0.110	2.880	0.970
Litter size	0.062	0.137	0.649
Model with significant traits:			
Constant	-193.150	0.228	0.000
Maternal hornedness	-0.441	0.188	0.019
Maternal year of birth	0.097	0.048	0.043

The logistic regression analysis showed that maternal hornedness and the year of birth were the only traits significantly influencing offspring sex ratio (Table 2), so the following regression equation can be written:

logit (Offspring sex ratio) = -193.15 – 0.441 × Maternal hornedness + 0.097 × Maternal year of birth.

The regression coefficient for hornedness is negative, thus possessing horns lowered the probability of delivering a daughter. Table 3 shows numbers and frequencies of kids with regard to their sex and maternal hornedness. From this table one can calculate that the proportion of daughters for mothers without horns is 0.622 and for mothers with horns – 0.522. The odds ratio for this trait equals 0.643.

Table 3
Numbers and frequencies of offspring grouped for their sex and mother's hornedness*

	Horns		
Sex of offspring	Absent	Present	Sums
Male	76 (15.38%)	140 (28.34%)	216 (43.72%)
Female	125 (25.30%)	153 (30.97%)	278 (56.28%)
Sums	201 (40.69%)	293 (59.31%)	494

*Besides, 13 mothers of unknown hornedness gave birth to 33 kids (17 sons and 16 daughters).

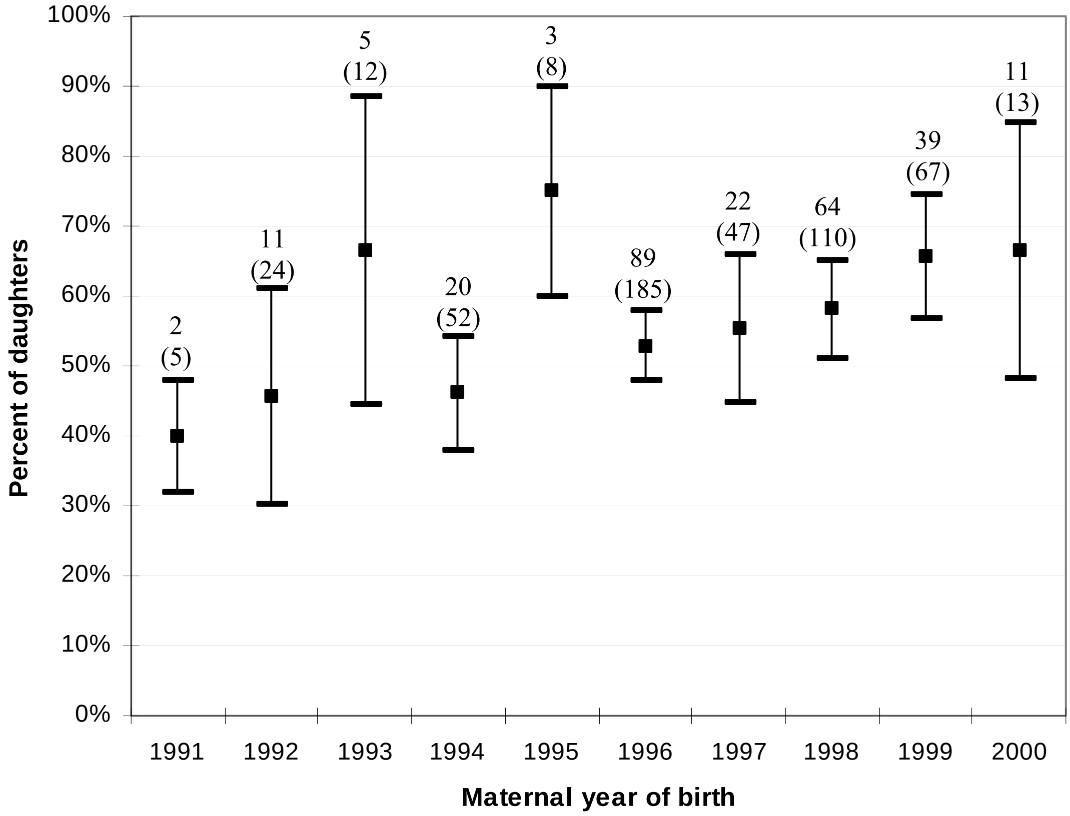

Fig.: Percentage of daughters (±1.96 × standard deviation) produced according to the maternal year of birth in domestic goats. The number of litters and, in parentheses, the number of kids are given for each category. Two mothers born in 2001, that gave birth to two kids, are excluded from the graph.

The regression coefficient for the maternal year of birth was positive, indicating an increased probability of bearing a daughter by mothers born later. The odds ratio for a one-year interval equals 1.102. Graph (Fig.) depicts sex ratio in categories of the

maternal year of birth. The Spearman rank correlation between the proportion of daughters and the maternal year of birth was $R = 0.142$ with $p = 0.020$. Mothers born in the years 1991-1994 descended mainly from the Jastrzębiec herd, mothers born after 1995 were chiefly from the Złotniki one. The Jastrzębiec mothers produced fewer daughters than the Złotniki ones ($p = 0.0093$ when testing the equality of proportions) and the proportion of daughters for the Złotniki mothers increased with the year of birth ($n = 171$, $R = 0.165$, $p = 0.031$). For the Złotniki mothers we also checked the correlation only for the first three litters in order to eliminate the effect of different age, and consequently a different number of litters of mothers born in various years. The result remained unchanged ($n = 152$, $R = 0.173$, $p = 0.034$).
Correlations between sex ratios in the consecutive litters were not significant. Only the correlation between the 1-st and 2-nd litter was marginally significant ($n = 57$, $R = -0.250$, $p = 0.061$).

Discussion

Offspring sex ratio in the study herd was female biased (55.8% female). WILLIAMS and RUDGE (1969) and BOYD (1981) did not observe any significant bias in the offspring sex ratio in the feral goat. However, these authors had small samples.
Maternal hornedness influenced offspring sex ratio in the study herd: horned females produced more sons than hornless ones. Hornedness affects the female domestic goat social rank: horned animals have a higher social status (HAFEZ et al., 1969; SAMBRAUS, 1971; BARROSO et al., 2000; GÓRECKI, 2001). Hence we can presume that dams of a higher rank produced more sons.
We stated that the year of the mother's birth influenced the offspring sex ratio. There are probably two reasons for this situation. First, dams came from different farms, where they might have had different environmental conditions. Goats from Jastrzębiec being the majority of dams born before 1995 produced more sons than goats from Złotniki being the majority of dams born after 1995. We suppose that the Jastrzębiec farm provided better conditions than the Złotniki one. Moreover, the proportion of daughters for dams born in Złotniki increased with their year of birth. Maternal age [...] the number of litter were not causes of this situation, as we stated analyzing only the first three litters. According to our knowledge about the Złotniki farm financial problems, the farm provided worse and worse conditions in the consecutive years. Thus, the results can point that environmental conditions provided to young female goats influence their long-term quality.
The results mentioned above are in agreement with the Trivers-Willard hypothesis, similarly to many authors' statements, for example: CASINELLO and GOMENDIO (1996, in *Ammotragus lervia*), CAMERON et al. [1999, in the feral horse (*Equus caballus*)], HEWISON et al. [1999, in the roe deer (*Capreolus capreolus*)], KOHLMANN [1999, in the red deer (*Cervus elaphus*)], CÔTÉ and FESTA-BIANCHET [2001, in the mountain goat (*Oreamnos americanus*)] and ENRIGHT et al. [2001, in the fallow deer (*Dama dama*)]. On the other hand, other authors, for example WOUTERS et al. (1995, in the roe deer) obtained results contrary to the Trivers-Willard model. In his paper KOJOLA (1997) stated that the results of studies on some cervids [red deer and reindeer (*Rangifer tarandus*)] supported the Trivers-Willard hypothesis, while on other cervids [moose (*Alces alces*), *Odocoileus hemionus* and *O. virginianus*] they were opposite.

BAKKEN (1998) revealed that silver fox (*Vulpes vulpes*) females with an improved man-animal relationship delivered more male cubs than others vixens did. Social dominance is also connected with better stress resistance as LYNCH et al. (1997) stated in the domestic sheep (*Ovis aries*). Thus, Bakken's results also support the Trivers-Willard model.

The marginally significant negative correlation between sex ratio in the first and in the second litter found in this study could be explained by the fact that the production of sons is more costly as CASINELLO (2001) stated in (*Ammotragus lervia*). MONARD et al. (1997) found that the production of a son in one year decreases this in the next year in feral horses. We did not observe such a correlation between later litters (e.g. the second and the third) possibly because older goats needed less resources for their own growth.

The kids in the study herd descended from parents of different breeds that differed in coat colour and physique, but the breed did not influence the offspring sex ratio. TRUT (1996) stated that the *star* gene (a semidominant coat colour mutation) affects offspring sex ratio in the silver fox.

Although female age influences her social rank in the domestic goat (SCOTT, 1948; ROSS and SCOTT, 1949; BARROSO et al., 2000; GÓRECKI, 2001), the domestic sheep (GRÄSER-HERMANN and SAMBRAUS, 2001) and the mountain goat (CÔTÉ and FESTA-BIANCHET, 2001), it had no significant effect in the study goat herd. CÔTÉ and FESTA-BIANCHET (2001) stated that older mountain goat females bear more sons. LANDETE-CASTILEJOS et al. (2001) found the opposite dependence in the mouflon (*Ovis musimon*).

The year of litter birth did not influence its sex ratio in this study in contrary to the results of MONARD et al. (1997). Yet the environmental conditions in nature are less stable than in a man-managed environment. Although conditions in Złotniki were not the same every year (as was discussed above), they were probably stable enough not to create differences in the offspring sex ratio among years.

We did not observe a significant influence of the litter size on its sex ratio in contrary to the statement by JACOBSEN et al. (1999) in case of humans (*Homo sapiens*).

In conclusion we can state that possessing horns by females lowered the proportion of daughters through the agency of social status. Also goats reared under better conditions (dependent on the farm and its financial condition in a given year) gave birth to fewer daughters. These results are in agreement with the Trivers-Willard model. Moreover, we observed a marginally significant negative correlation between sex ratio in the first and in the second litter.

References

BAKKEN, M.:
The effect of an improved man-animal relationship on sex ratio in litters and on growth and behaviour in cubs among farmed silver fox (*Vulpes vulpes*). Appl. Anim. Behav. Sci., **56** (1998), 309-317

BARROSO, F.G.; ALADOS, C.L.; BOZA, J.:
Social hierarchy in the domestic goat: effect on food habits and production. Appl. Anim. Behav. Sci., **69** (2000), 35-53

BOYD, I.L.:
Population changes and the distribution of a herd of feral goats (*Capra* sp.) on Rhum, Inner Hebrides, 1960-1978. J. Zool., Lond., **193** (1981), 287-304

CAMERON, E.Z.; LINKLATER, W.L.; STAFFORD, K.J.; VELTMAN, C.J.:

Birth sex ratios relate to mare condition at conception in Kaimanawa horses. Behav. Ecol., **10** (1999), 472-475
CASINELLO, J.:
Offspring grazing and suckling rates in a sexually dimorphic ungulate with biased maternal investment (*Ammotragus lervia*). Ethology, **107** (2001), 173-182
CASINELLO, J.; GOMENDIO, M.:
Adaptive variation in litter size and sex ratio at birth in a sexually dimorphic ungulate. Proc. R. Soc. London-Ser. B, **263** (1996), 1461-1466
CLARK, A.B.:
Sex ratio and local resource competition in a Prosimian primate. Science, **201** (1978), 163-165
CÔTÉ, S.D.; FESTA-BIANCHET, M.:
Offspring sex ratio in relation to maternal age and social rank in mountain goat (*Oreamnos americanus*). Behav. Ecol. Sociobiol, **49** (2001), 260-265
ENRIGHT, W.J.; SPICER, L.J.; KELLY, M.; CULLETON, N.; PRENDIVILLE, D.J.:
Energy level in winter diets in Fallow deer: Effect on plasma insuline-like growth factor I and sex ratio of their offspring. Small Ruminant Res., **39** (2001), 253-259
GÓRECKI, M.T.:
Zachowania społeczne samic kozy domowej (*Capra hircus* Linnaeus, 1758) utrzymywanych w chowie alkierzowym [Polish] (On social behaviour of female domestic goats (*Capra hircus* Linnaeus, 1758) kept indoor). PhD thesis, August Cieszkowski Agricultural University of Poznań, 2001
GRAFFELMAN, J.; HOEKSTRA, R.F.:
A statistical analysis of the effect of warfare on the human secondary sex ratio. Hum. Biol., **72** (2000), 433-445
GRÄSER-HERRMANN, C.; SAMBRAUS, H.H.:
The social behaviour of East Friesian dairy sheep in larger groups. Arch. Tierz., Dummerstorf **44** (2001), 421-423
HAFEZ, E.S.E.; CAIRNS, R.B.; HULET, C.V.; SCOTT, J.P.:
The behaviour of sheep and goats. In: Hafez, E.S.E.(Ed), Behavior of domestic animals. Bailliere Tyndall and Cox, London, (1969), 296-348
HEWISON, A.J.M.; ANDERSEN, R.; GAILLARD, J.M.; LINNELL, J.D.C.; DELORME, D.:
Contradictory findings in studies of sex ratio variation in roe deer (*Capreolus capreolus*). Behav. Ecol. Sociobiol., **45** (1999), 339-348
JACOBSEN, R.; MOLLER, H.; MOURITSEN, A.:
Natural variation in the human sex ratio. Hum. Reprod., **14** (1999), 3120-3125
KOHLMANN, S.G.:
Adaptive fetal sex allocation in elk: evidence and implications. J. Wild Manage., **63** (1999), 1109-1117
KOJOLA, I.:
Social status and physical condition of mother and sex ratio of offspring in cervids. Appl. Anim. Behav. Sci., **51** (1997), 267-274
KRUUK, L.E.B.; CLUTTON-BROCK, T.H.; ALBON, S.D.; PEMBERTON, J.M.; GUINNESS, F.E.:
Population density affects sex ratio variation in red deer. Nature, **399** (1999), 459-461
LANDETE-CASTILEJOS, T.; GARCIA, A.; LANGTON, S.; INGLIS, I.; GALLEGO, L.; GARDE, J.:
Opposing offspring sex ratio variation with increasing age and weight in mouflon mothers (*Ovis musimon*). Acta Vet. Hung., **49** (2001), 257-268
LYNCH, J.J.; HINCH, G.N.; ADAMS, D.B.:
The behaviour of sheep. Biological principles and implications for production. CSIRO Publications, East Melbourne, (1992)
MILLESI, E.; HUBER, S.; EVERTS, L.G.; DITTAMI, J.P.:
Reproductive decisions in female European ground squirrel: Factor affecting reproductive output and maternal investment. Ethology, **105** (1999), 163-175
MONARD, A.M.; DUNCAN, P.; FRITZ, H.; FEH, C.:
Variations in the birth sex ratio and neonatal mortality in a natural herd of horses. Behav. Ecol. Sociobiol., **41** (1997), 243-249
MYSTERUD, A.; YOCCOZ, N.G.; STENSETH, N.C.; LANGVATN, R.:
Relationship between sex ratio, climate and density in red deer: The importance of spatial scale. J. Anim. Ecol., **69** (2000), 957-974
NICOLICH, M.J.; HUEBNER, W.W.; SCHNATTER, A.R.:
Influence of parental and biological factors on the male birth fraction in the United States: an analysis of birth certificate data from 1964 through 1988. Fertil. Steril., **73** (2000), 487-492
NONAKA, K.; DESJARDINS, B.; CHARBONNEAU, H.; LEGARE, J.; MIURA, T.:
Human sex ratio at birth and mother's birth season: Multivariate analysis. Hum. Biol., **71** (1999), 875-884

NOWAK, R. M.:
Walker's Mammals of the world. The John Hopkins University Press, Baltimore and London, 1999
NUNN, C.L.; PEREIRA, M.E.:
Group histories and offspring sex ratio in ringtailed lemurs (*Lemur catta*). Behav. Ecol. Sociobiol., **48** (2000), 18-28
ROSS, S.; SCOTT, J.P.:
Relationship between dominance and control of movement in goats. J. comp. physiol. Psychol., **42** (1949), 75-80
SAMBRAUS, H.H.:
Das Sozialverhalten von domestizieren Ziegen. Z. Säugetierk., **36** (1971), 220-24
SCOTT, J.P.:
Dominance and the frustration-aggression hypothesis. Physiol. Zool., **21** (1948), 31-39
SILK, J.B.:
Local resource competition and facultative adjustment of sex ratio in relation to competitive abilities. Am. Nat., **121** (1983), 56-66
StatSoft, Inc.,
2000. STATISTICA for Windows [Computer program manual]. Tulsa, OK.
TRIVERS, R.L.; WILLARD, D.E.:
Natural selection of parental ability to vary the sex ratio of offspring. Science., **179** (1973), 90-92
TRUT, L.N.:
Sex ratio in silver foxes: effect on domestication and the *star gene*. Theor. Appl. Genet., **92** (1996), 109-115
WAUTERS, L.A.; DE CRUMBRUGGHE, S.A.; NOUR, N.; MATTHYSEN, E.:
Do female roe deer in good condition produce more sons than daughters. Behav. Ecol. Sociobiol., **37** (1995), 189-193
WILLIAMS, G.R.; RUDGE, M.R.:
A population study of feral goats (*Capra hircus* L.), from Macauley Island, New Zealand. Proc. N.Z. Ecol. Soc., **16** (1969), 17-28

Received: 2002-11-13

Accepted: 2003-05-07

Authors' addresses
Assistant Professor MARCIN TADEUSZ GÓRECKI, PhD.
Department of Sheep and Goat Breeding
August Cieszkowski Agricultural University of Poznań
Słoneczna 1, Złotniki,
62-002 Suchy Las
Poland

E-Mail: marcing@owl.au.poznan.pl

Assistant Professor KRZYSZTOF KOŚCIŃSKI, PhD.
Department of Human Biological Development
Institute of Anthropology
Adam Mickiewicz University
Fredry 10,
61-701 Poznań
Poland

E-Mail: krzychu@amu.edu.pl