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Source: Wildlife Biology, 10(2) : 137-143

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2004.018

Alpine ibex *Capra ibex ibex* x domestic goat *C. aegagrus domestica* hybrids in a restricted area of southern Switzerland

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Giacometti, M., Roganti, R., De Tann, D., Stahlberger-Saitbekova, N. & Obexer-Ruff, G. 2004: Alpine ibex *Capra ibex ibex* x domestic goat *C. aegagrus domestica* hybrids in a restricted area of southern Switzerland. - Wildl. Biol. 10: 137-143.

We documented hybridisation of domestic goats *Capra aegagrus domestica* with free-ranging male Alpine ibex *Capra ibex ibex* in a restricted area of the southern Swiss Alps in 1989-2001. The number of animals in the hybrid herd reached a maximum of 18 in 1998. We confirmed hybridisation through morphological data and genetic analysis. All presumed hybrids were larger and heavier than Alpine ibex. Horns of hybrids were longer than those of Alpine ibex, and some male horns lacked nodes. In two males studied, the first horn increment was longer than the second. In some cases the pelage colour revealed characteristics untypical for ibex such as prominent leg markings and dark brown colour in young animals. Microsatellite analysis in one male revealed ibex specific alleles as well as goat specific alleles. We concluded that this male, as well as the other animals studied, were Alpine ibex x domestic goat hybrids. All wild goats and their hybrid offspring were removed by state gamekeepers in 1998-2001 to maintain the genetic integrity of free-ranging Alpine ibex living in the area. We suggest that the survival of hybrids depends largely on habitat characteristics. In the study area, the hybrid winter range was exposed to the south. The sunny rocky slope was steep and reached down to an altitude of 1,500 m a.s.l. On this slope, animals found food in early spring and a refuge against adverse weather conditions.

Key words: Alpine ibex, domestic goat, hybridisation, habitat, management, microsatellite analysis, morphology

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Received 9 May 2003, accepted 11 August 2003

Associate Editor: Marco Festa-Bianchet

Alpine ibex *Capra ibex ibex* of both sexes can hybridise with domestic goats *Capra aegagrus domestica* in captivity (Bächler 1918, Stüwe & Grodinsky 1987). In F1 hybrids, body size and shape are intermediate between the two species. The coat may show dark or light colour spots and bands. The horns of male hybrids have smaller nodes and are generally longer than in Alpine ibex. Hybrids of both sexes are fertile (Couturier 1962).

In the 18th and 19th century, when Alpine ibex was extinct in most of the Alps, crossing of ibex with domestic goats was common in parks and zoological gardens throughout central Europe. Release of captive hybrids in nature occurred in several regions of the central and eastern Alps until 1903 in attempts to reestablish the 'species' in its original habitat (Bächler 1935, Ausserer 1947). However, these introductions were unsuccessful. After 1911, when pure Alpine ibex bred in the park Peter and Paul in St. Gallen became available for translocations, crossing of ibex with goats in parks became useless (Giacometti 2003).

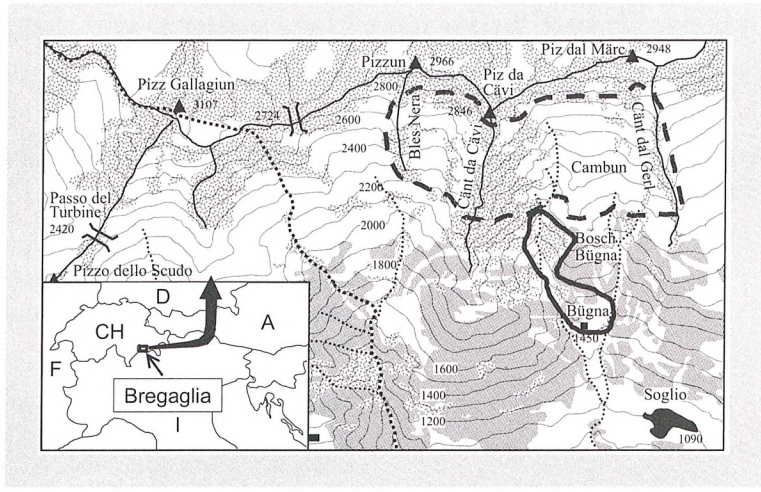

Figure 1. Location of the Bregaglia valley in the central Alps (Grisons, Switzerland), and the domestic goat x Alpine ibex hybrid habitat during 1989-2001. The dotted diagonal line in the left part of the figure represents the Swiss-Italian state border. The broken line in the right half of the figure demarcates the summer range, the solid line the winter range. Dotted surfaces represent rocky areas, grey surfaces are wood. Numbers represent altitudes, triangles peaks, intermediate solid lines mountain crests, and fine solid lines represent contour lines.

Free-ranging Alpine ibex breed in December-January, and kids are mostly born in the beginning of June (Giacometti & Ratti 1994). In contrast, domestic goats and hybrids conceive earlier, and parturition occurs in February-May (Bächler 1918, Stämpfli 1979, Stüwe & Grodinsky 1987, Gall 2001). Early parturition was considered to be the major cause of failure of hybrid reintroduction programmes in the Swiss Alps in the second half of the 19th century (Bächler 1918, Couturier 1962). Hybrid kid survival in nature was thought to be impossible when the ambient temperature is low and snow may still be present in the wintering areas (Stüwe & Grodinsky 1987). In the Bregaglia valley, however, a region situated in the south central Alps, escaped domestic goats bred with free-ranging male Alpine ibex, and some F1 hybrids survived. After reaching sexual maturity, F1 females bred with male ibex, and a small domestic goat and hybrid herd developed during 1989-2001.

The aims of this study are: a) to document the exceptional survival of free-ranging Alpine ibex x domestic goat hybrids in a restricted Alpine area without artificial feeding; b) to describe the habitat used by female domestic goats (which became wild) and their hybrid offspring; c) to describe selected morphological aspects of the hybrids; and d) to verify hybridisation of one male by microsatellite analysis.

Material and methods

Study area

The Bregaglia valley (46°17'-46°26'N, 9°27'-9°47'E) is situated in Grisons, a Canton in southeastern Switzerland (Fig. 1). It is a 252 km^2 deep alpine valley with the main river Maira running in a southwesterly direction. The Bregaglia valley is characterised by an insubric alpine, Mediterranean influenced climate. Mean annual precipitation is 1,400 mm at 1,100 m a.s.l., with most precipitation recorded during May, August and October. January is the coldest month (0°C-isotherm at 600 m a.s.l.) and July the warmest month (0°C-isotherm at 3,500 m a.s.l.). At 1,100 m a.s.l., a mean of 113 frost days and eight days with temperature at times > 25°C are recorded annually (Gensler 1978). Deciduous forest of mainly oak *Quercus petraea*, lime *Tilia cordata*, birch *Betula pendula* and aspen *Populus tremula* occurs up to 1,400 m a.s.l. on the south-exposed mountain slope. At higher elevations up to the treeline at 2,000 m a.s.l., spruce *Picea abies* is the most common tree. Common shrubs are juniper *Juniperus* and bilberry *Vaccinium*. Alpine meadows are dominated by crooked sedge-grass *Caricetum curvulae* and mat-grass *Nardetum stricta* (Stampa & Maurizio 1994, R. Maurizio, pers. comm.).

The Alpine ibex x domestic goat hybrid habitat is situ-

ated north of Soglio, a village on a southern, sunny mountain slope. In particular, the area south of Piz da Cävi is characterised by a rocky, steep hillside reaching from 2,850 m down to 1,500 m a.s.l.. The overall mean slope is 38°, with mean values reaching 47° on the southeastern face of Piz da Cävi. The annual mean number of hours with sunshine in Soglio (at 1,090 m a.s.l.) is 3,370 hours, with maxima in spring (1,040 hours) and summer (1,161 hours; Schweizer 1991).

History of hybrids

In the summer of 1989, a farmer put his domestic goat herd on an alpine pasture in the area south of Passo del Turbine in the Community of Villa di Chiavenna, Italy. The composition of the goat herd was mixed, original breeds being mainly Grisons striped and Chamois coloured. The goats were left alone during the grazing period. During this period, five females moved westward and reached Bügna in the Community of Soglio, Switzerland, approximately 3 km from their designated summer pasture. Here, the goats selected a suitable winter range where they spent the next winter period at 1,400-1,800 m a.s.l. During the summer of 1990, the goats moved west, towards Cant da Cävi and Bles Nera, but they remained in the Swiss part of the study area. The goats spent the winter 1990/91 in Bügna, and in the summer of 1991 they moved back to Cänt da Cävi/Bles Nera. By then, all of them were followed by a kid. Of these five kids, four, all males, were captured by Italian farmers, castrated and kept together with the goat herd. The kids showed morphological characteristics of both domestic goat and ibex. Hence, the female goats must have bred with male ibex during the late summer/autumn of 1990.

In late autumn 1991, the same five goats moved back to their now traditional winter range. In the following winters, the goats and their hybrid offspring switched to a slightly higher rocky winter range west of Bosch Bügna (at 1,500-2,000 m a.s.l.). The approximately 2.5 km^2 summer range was located in higher regions (at 1,900-2,800 m a.s.l.) and extended from Bles Nera in the west to Cänt dal Gerl in the east. The wild goats did not associate with free-ranging ibex females that used part of their range. In August-October, however, goats and hybrids were at times seen with ibex males, mostly in the Cambun area. Newborn hybrids were seen in March-May.

The number of animals in the hybrid herd peaked at 18 in 1998. From 1991 to 2001, a total of 10 male hybrids were captured by Italian farmers for meat production. One domestic goat was found dead in 1993 in Bosch Bügna, in 1995 another (together with three hybrids) was struck by lightning in Cänt dal Gerl, and an unknown number of hybrids have died from natural causes. Finally, 18 animals (three domestic goats and 15 hybrids) were shot by Swiss state gamekeepers during 1998-2001 to eliminate the hybrid herd. Shooting them was difficult because the hybrids ran into rocky areas when they saw people, and continued to escape for hundreds of metres until they disappeared. All goats and hybrids were shot by 22 October 2001.

Morphology of hybrids

Of the 15 hybrids shot by the state gamekeepers, seven were measured and weighted. We measured body length, shoulder height, chest girth, hind foot length, horn length, annual horn increments and goatee beard length as described in Giacometti, Bassano, Peracino & Ratti (1997) and Giacometti & Ratti (2003). Body weight refers to field-dressed animals, which corresponds to approximately 70% of their live weights. We compared biometric data of hybrids with mean values for Alpine ibex of the same sex and age shot during October 1977-1999 in Grisons (Giacometti & Ratti 2003). Finally, we documented the morphology of hybrid horns and described selected morphological criteria of the pelage.

Tissue sampling, DNA extraction and microsatellite markers

For our genetic analysis we selected microsatellites common throughout the mammalian genome and which have been used in previous genetic studies of domestic and wild ruminants (Luikart, Biju-Duval, Ertugrul, Zagdsuren, Maudet & Taberlet 1999, Maudet, Luikart & Taberlet 2001). The genetic markers we used are known to be most suitable for analysis of hybridisation events as described in other species such as hare *Lepus* spp. (Andersson, Thulin & Tegelstrom 1999) and wolf *Canis* spp. (Dolf, Schläpfer, Gaillard, Randi, Lucchini, Breitenmoser & Stahlberger-Saitbekova 2000). More-

Table 1. The 10 *loci* selected for microsatellite analysis in a 3.3-year old male from Bregaglia (Grisons, Switzerland) presumed to be an F2 domestic goat x Alpine ibex hybrid.

	Range		Genotype hybrid	
SSR locus	Goat	Ibex	Goat allele	Ibex allele
DRBP1	196-228	no amplification	196bp	
ILSTS029	154-180	173-175	154bp	174bp
P19	176-202	169 MM	193bp	169bp
TGLA122	127-139	137-157	127bp	153bp
IL12p35	133-137	129 MM	133bp	129bp
INRA063	164-168	154 MM		154bp
076MILSTS	116-130	136-152		136bp
BOBT24	151-175	143 MM		143bp
INFgamma	186-198	190 MM		190bp MM
NRAMP1	185-189	191 MM	189bp	

MM: indicates monomorphic alleles

Table 2. Biometric data of seven domestic goat x Alpine ibex hybrids shot by the state gamekeepers during 1998-2001 in Bregaglia (Grisons, Switzerland). BW = body weight (in kg), BL = body length (in cm), CH = shoulder height (in cm), CM = chest girth (in cm), HFL = hind foot length (in cm), HL = horn length (in cm), and the percentage values represent comparison with mean values recorded in Alpine ibex shot in October 1977-1999 in Grisons as reported by Giacometti & Ratti (2003).

Animal No	Date	Sex	Age	BW	%	BL	%	CH	%	CM	%	HFL	%	HL	%
1	22.10.2001	♀	0.5	10	114							25	108	9	143
2	13.10.1998	♀	1.5	27	158	124	114	75	112	75	112	29	107	26.3	193
3	13.10.1998	♀	1.5	25	146	124	114	74	110	72	107	30	110	21.5	158
4	22.10.2001	♀	4.5	32	111							31	106	28.8	133
5	22.10.2001	♂	0.5	12	111							25.5	106	12	129
6	13.10.1998	♂	0.5	18	167	115	122	68	117	64	116	28.5	118	12.7	137
7	07.08.2000	♂	3.3	45	152	153	113	91	108	92	107	33.5	104	51.8	131

over, markers developed for the domestic goat can be successfully applied to study wild taxa (Maudet et al. 2001).

We sampled a 3-year old male presumed to be a hybrid, shot on 7 August 2000 in Cambun in the community of Soglio at 2,500 m a.s.l. A muscle sample of the diaphragm was collected and frozen at -18°C. DNA was extracted from ~20 mg of tissue using the DNeasy™ Kit (QIAGEN GmbH, Germany) following the manufacturer's procedures. We selected 10 primers based on results of previous studies of domestic goat and Alpine ibex (Saitbekova, Gaillard, Obexer-Ruff & Dolf 1999, Maudet, Miller, Bassano, Breitenmoser-Wursten, Gauthier, Obexer-Ruff, Michallet, Taberlet & Luikart 2002, G. Obexer-Ruff & M-L. Glowatzky-Mullis, unpubl. data), and considered *loci* with species specific alleles for both species as well as alleles showing non-overlapping ranges in both species (Table 1). PCR products were electrophoresed on a 6% denaturing polyacrylamide gel on an ABI Prism 377 automated sequencer (Perkin Elmer).

Figure 2. Right horns of three males in their fourth year of life from Bregaglia (Grisons, Switzerland). From left to right: a pure Alpine ibex (*Capra i. ibex*), an F2 and an F1 hybrid Alpine ibex x domestic goat hybrid, respectively.

Results

Morphology

Hybrids of both sexes were larger than the ibex in Grisons (Table 2). Horn length and body weight reached 193% and 167% of ibex values, respectively. A 3.3-year old male (animal # 7) shot in August weighted 45 kg, which is similar to the mean weight of 4.5-year old male ibex in October. Mean values of body length, shoulder height and chest girth were > 110%, and hind foot length was 104-110% of mean ibex values. Horns of an F1 and of an F2 male hybrid from Bregaglia as well as of an Alpine ibex male (all animals in their fourth year of life) are shown in Figure 2. In the F1 hybrid captured by farmers and subsequently slaughtered (additional data not available), the scimitar-shaped, sharp-keeled horns were laterally flattened, and the anterior sweep was broken by occasional flattened knobs. Annual horn increments and total horn length are reported in Table 3. In the second male (animal # 7) presumed to be a F2 hybrid, the horn core cross-section was roundish with narrow facial and caudal features. Two flat and four distinct, rounded knobs were formed. The first knob was in the first horn increment, which is unusual in ibex. In the pure Alpine ibex horn shown for comparison, the cross-section was rectangular with longer lateral surfaces. Five distinct knobs in the second-fourth increments were formed. These were narrower than in the F2 hybrid.

Table 3. Horn measurements (in cm) of one F1 and one F2 goat x Alpine ibex hybrids (both males) in Bregaglia (Grisons, Switzerland). HG1-HG3 = annual horn growth in the first, second and third year of life, respectively. HL4 = total horn length in the fourth year of life, and the percentage values represent comparison with mean values recorded in Alpine ibex shot during October 1977-1999 in Grisons as reported by Giacometti & Ratti (2003).

	F1	%	F2	%	Alpine ibex $\bar{x}$	SD	N
HG1	17.0	239.4	16.0	225.4	7.1	2.2	5415
HG2	16.6	176.6	10.3	109.6	9.4	1.8	5442
HG3	13.4	161.4	11.5	138.6	8.3	1.4	5409
HL4	67.0	170.1	50.0	126.9	39.4	3.9	1332

Hybrids were brownish, dark brown or greyish with white undersides. The leg markings were more prominent than in Alpine ibex: the front side of each leg was dark brown, whereas the back sides were white. Hybrids shot in October lacked wool hair which is typically found in the winter coat of Alpine ibex. The goatee beard of male # 7 was 14.3 cm long which is > 200% of ibex values. Female hybrids lacked beards.

Microsatellite DNA analysis

In animal # 7, three *loci* (INRA063, 076MILSTS and BOBT24) showed ibex specific alleles (see Table 1). INFgamma was monomorphic (which is typical for Alpine ibex and unusual in goats), but we can not exclude the possibility that the INFgamma originated from the goat gene pool. Four other *loci* showed one ibex specific and one goat specific allele (ILSTS029, P19, TGLA122 and IL12p35). Finally, two primers amplified goat specific alleles (DRBP1, NRAMP1). For DRBP1, the goat primers do not amplify in ibex, suggesting a mutation in the ibex sequence for this *locus*. Therefore, animal # 7 definitely contained goat genes.

Discussion

We have documented mating of domestic goats with free-ranging male ibex in a restricted area of the southern Swiss Alps during 1989-2001. We believe that this is the first report on the survival of hybrids born in nature and of the establishment of a free-ranging domestic goat x Alpine ibex hybrid herd without supplied artificial feeding. All wild goats and their hybrid offspring were removed by state gamekeepers during 1998-2001 to maintain genetic integrity of free-ranging Alpine ibex. Survival of hybrids in early spring may depend largely on the habitat characteristic. In Bregaglia, the winter range was exposed to the south and sunny. The rocky slope was steep and reached down to an altitude of 1,500 m a.s.l. On the slope, animals found a refuge against adverse weather conditions and human disturbance. Snow cover is usually short lasting, and vegetation growth starts in April. In Arosa (Grisons), where hybrids were released during 1879-1885 (Bächler 1918), south-exposed, rocky slopes are limited, and the mean number of hours with sunshine is clearly lower than in Bregaglia (1,818 per year and 503 in spring; Gensler 1978).

The five female domestic goats and their offspring occupied a region populated by free-ranging Alpine ibex, but they did not associate with ibex females. According to Schaller (1989), this social avoidance could be explained in evolutionary terms. Natural selection would tend to separate two different species and strengthen barriers in gene flow. However, the partial isolation of hybrids and pure ibex may partially be due to social factors. The historical introduction of Alpine ibex suggests that animals released in the same place and at the same time, but which come from different parks and therefore do not know each other, tend to colonise different areas (Bächler 1935).

All presumed hybrids were larger and heavier than Alpine ibex. The pelage colour revealed in some cases characteristics atypical for Alpine ibex, such as prominent leg markings and dark brown colour in young animals (Couturier 1962). In hybrids, horns were longer than in Alpine ibex. In some cases, male horns lacked the nodes typically found in male ibex older than one year (Nievergelt 1978), and horn core cross-sections resembled the horns of domestic or wild goats as described by Schaller (1989). In two males studied, the first horn increment was longer than the second, which is in contrast to what is generally seen in Alpine ibex (Giacometti, Willing & Defila 2002).

This case of hybridisation in Bregaglia does not imply that free-ranging Alpine ibex in the Swiss Alps interbreed with domestic goats. Studies evaluating the genetic variability of Alpine ibex did not reveal hybridisation (Hartl 1986, Stüwe & Scribner 1989, Maudet et al. 2002). In particular, Albris and Augstmatthorn populations, which together with the Mont Pleureur population are the founder populations of the majority of the Swiss ibex populations (Giacometti 2003), were found to belong to the common group Gran Paradiso, which is the source population of all existing Alpine ibex. Randi, Tosi, Toso, Lorenzini & Fusco (1990) documented a higher genetic variability in the Albris than in the Gran Paradiso population. Although no goat gene was found, the before-mentioned authors suggested that Albris ibex may have interbred with domestic goats. In contrast, Maudet et al. (2002) revealed a higher variability in the Gran Paradiso ibex than in the Albris ibex. Therefore, the results of Randi et al. (1990) were more likely due to inappropriate sampling of the Gran Paradiso population rather than to hybridisation of the Albris ibex. However, it can not be ruled out that somewhere in the Alps, particularly in the climatically more favourable southern parts, domestic goat x Alpine ibex hybrids may survive. As F2 and F3 hybrids may be difficult to distinguish morphologically from pure ibex (Fitzinger 1864, our data), hybridisation may remain undiscovered when field surveys are performed inappropriately.

During the last decades, sporadic cases of hybridisation between domestic goat and free-ranging Alpine

ibex have been observed in different locations in the Alps (e.g. in Aosta, Glarus, Grisons, Piedmont, Sondrio, Ticino and Valais). In these cases, however, domestic goat females mated with juvenile male ibex that joined the goat herds in summer or autumn, and offspring were born in captivity. Unfortunately, these ibex x domestic goat hybrids have only been reported sporadically in the scientific literature (Stämpfli 1979).

In conclusion, we have shown that under particular circumstances domestic goat x Alpine ibex hybrids may survive and breed in nature in the Alps. Maintaining the genetic integrity of Caprinae as recommended by the IUCN/SSC Caprinae Specialist Group should therefore not only include appropriate reintroduction policies as suggested by Shackleton (1997), but also policies on how to avoid hybridisation and removal of hybrids from nature. In addition, physical contact associated with breeding may lead to interspecific transmission of infectious agents such as *Brucella melitensis* causing brucellosis (Ferroglio, Tolari, Bollo & Bassano 1998) or *Sarcoptes scabiei* causing sarcoptic mange (León-Vizcaíno, Ruíz de Ybáñez, Cubero, Ortíz, Espinosa, Pérez, Simón & Alonso 1999). We therefore suggest that domestic goat herds be tended carefully during the grazing period and that goats that have escaped into alpine pastures be removed. Finally, field surveys for morphological traits typical of hybrids should be performed in areas where hybridisation is suspected.

Acknowledgements - we express our gratitude to Peider Ratti and Jürg Brosi who initiated and supported this study. Special thanks go to Remo Maurizio for his useful contribution in the habitat description, to Erwin Eggenberger for providing ibex data from Grisons, to Marie-Louise Glowatzky-Mullis for valuable scientific support and to Peter Lüps for providing literature. Finally, we thank Marco Festa-Bianchet, John Wehausen and Achaz von Hardenberg for valuable comments on a previous version of the manuscript. This study was part of the Interreg III A Project on Extensive Grazing of Sheep and Goats in Grisons (Switzerland) and Sondrio (Italy) and of the Research Project on Infectious Keratoconjunctivitis, Chur (Switzerland).

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