COHORT AFFECTS GROWTH OF MALES BUT NOT FEMALES IN ALPINE IBEX (*CAPRA IBEX IBEX*)

C. Toïgo, J.-M. Gaillard, and J. Michallet

Unité Mixte de Rercherche 5558, Biométrie, Génétique, et Biologie des Populations, Université Claude Bernard, Lyon1, 43 boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France (CTO, JMG)

Office National de la Chasse. Centre National d'Etudes et de Recherche Appliquée sur la Faune de Montagne, 8 impasse Champ Fila, 38320 Eybens, France (CTO, JMI)

We studied long-term cohort effects on chest girth and horn length in a recently established population of alpine ibex (*Capra ibex ibex*). Environmental conditions of the year of birth affected chest girth and first-annual increment of horns of males but did not affect chest girth and horns of females. Females compensated for a slow horn growth during their 1st year of life, whereas males did not. Level of polygyny of the species and environmental conditions experienced by the population could account for the occurrence of long-term cohort effects in male growth and its absence in female growth. Abundance of food resources throughout the study period allowed females to show compensatory growth. However, evolutionary constraints on growth that may exist in males of polygynous species may have prevented males from showing compensatory growth.

Key words: *Capra ibex ibex,* horn length, chest girth, cohort, sexual selection

Recent studies on ungulates have emphasized the importance of cohort effects (influence of the year of birth) on several life-history traits, including birth weight, postnatal growth rate, survival rate during the first winter, age of first reproduction, and adult survival (e.g., Albon et al., 1987; Andersen and Linnell, 1997; Gaillard et al., 1993*a*). Cohort effects generally are considered to act through environmental factors influencing maternal condition that determines quality and quantity of early maternal care. These result in variations in birth weight and postnatal growth rate. Environmental conditions during the year of birth may have short or long-term effects. Short-term cohort effects result in numerical effects by determining number of individuals of a cohort to be recruited in the population, whereas long-term effects influence phenotypic quality of adults and thereby may determine reproductive success of individuals from a cohort (Albon et al., 1992; Gaillard et al., 1997).

Among the studies focusing on cohort effects, some have observed long-term effects (Albon et al., 1992; Festa-Bianchet et al., 1994; Gaillard et al., 1997; Shultz and Johnson, 1995) and others have not (Albon et al., 1992; Bunnell, 1978; Gaillard et al., 1993*b*, 1997; Verme, 1963). To account for these differences, two non-exclusive causes have been proposed. First, environmental conditions can be involved. When resources are not sufficient, individuals may not be able to compensate for initial growth disadvantages and conditions experienced during early life may affect an individual's phenotypic characteristics throughout life (Albon et al., 1992; Gaillard et al., 1993*b*; Krebs and Cowan, 1962). Second, level of polygyny and the associated constraints on differential maternal care (Pélabon, 1997) may account for differential cohort effects according to sex. When between-sex differences occur in maternal care, extra care of male offspring would provide a fitness advantage to females in higher than average body condition (Clutton-Brock, 1991; Maynard-Smith, 1980; Trivers and Willard, 1973). In species with limited sexual selection, similar extra maternal care toward male offspring would not provide any fitness advantage to mothers in better than average condition (Hewison and Gaillard, 1996; Verme, 1983). Thus, occurrence of long-term cohort effects in male phenotypic quality could be related to the level of polygyny of the species and occurrence of male-biased maternal care.

In a recently introduced population of alpine ibex (*Capra ibex ibex*), we investigated cohort effects on yearling and adult phenotypic quality by using chest-girth and horn-growth measurements. Ibex are polygynous with substantial sexual dimorphism (Couturier, 1962). We tested the following hypotheses. First, because the population did not face food constraints, we expected male and female ibex to be able to compensate for early growth disadvantages. Thus, if long-term cohort effects were caused by food shortage, we did not expect them to affect this ibex population. Second, if long-term cohort effects were related to selection on differential maternal care, we expected male ibex to be affected by cohort conditions throughout life, and no prediction could be stated for females. Finally, if both food availability and selection on maternal care played a role, we expected long-term cohort effects to act on males more strongly than on females.

Material and Methods

Study area.—The study area was the Belledonne-Sept-Laux Reserve (Isère, France), managed by the Office National de la Chasse (O.N.C.). The Belledonne massif is situated between the Prealps (Chartreuse, Vercors) and the intern Alpine arc. Mean annual temperature was 6°C, and precipitation averaged 1,700 mm/year at 1,000 m above sea level, including substantial snow cover. Mean elevation of the study site is 2,200 m. Most areas occupied by ibex were east and south facing, and mean slope was steep (ca. 90%). We distinguished three habitats. The mountain range between 1,000 m and 1,600 m was characterized by spruce (*Picea abies*) and beech (*Fagus sylvatica*)–spruce forests. Sub-alpine range between 1,600 m and 2,200 m was dominated by bushes (*Rhododendron, Vaccinium,* and *Juniperus*) or meadows with *Pinus uncinata* and *P. cembro.* Alpine ranges with meadows above 2,200 m were characterized by meadows (Michallet et al., 1988).

Population and site.—The ibex population was founded in 1983, with 13 females and 7 males from the Mont-Pleureur Reserve (Switzerland). After introduction, the population increased and reached ca. 350 animals by summer 1994. Over 50% of 2-year-old females and >80% of females older than 2 years of age had young at heel every year (J. Michallet, in litt.).

Ibex have been captured and ear-tagged since 1986. Animals were captured using several methods (capture-gun, cage-trap, and leg-snare) approved by the French Environment Ministry. At capture, we measured length of both horns and chest girth to the nearest 5 mm. We separated horn length into two parts: first-annual increment and total horn length minus first-annual increment (adult horn length). For each individual, we used the maximum of both horns. Because chest girth and adult horn length are influenced strongly by age (Couturier, 1962), all analyses on those measures were performed accounting for the effect of log-transformed age. Annual increment was the distance between two consecutive annuli, represented by straight lines perpendicular to the horn and well visible on the horn back. Using those annuli, we determined age of captured animals and back-calculated to year of birth. We conducted separate analyses for males and females. We used the first increments of males and females aged ≤5 years, but not older (because first-annual increment wears with increasing age). Horns of females were much shorter than those of males and increments tend to become smaller and less visible. However, increments are well marked until 4 years of age. Thus, to overcome possible uncertainties about cohort determination, we reinforced analyses on females with analyses using only females aged 1–4 at capture. All animals were born in the reserve in 1984–1995, and 12 cohorts were represented for each sex.

Meteorological data.—We used meteorological data from the Rivier d'Allemont station compiled by the French National Meteorological Center, Météo France. The Rivier d'Allemont is only 3 km from the reserve at an elevation of 1,260 m. In temperate mountains like the Alps, influence of weather on life-history traits is likely greatest during winter (when access to vegetation is limited by snow cover), and spring (when plant growth determines food quantity and quality). Specifically, we examined mean snow cover during winter prior to birth (December–February), mean temperature during spring of birth (April–June), total precipitation during spring of birth (April–June), and mean snow cover in April prior to birth.

Data analyses.—To examine if effects of age and cohort affected chest girth or adult horn lengths, we first conducted an analysis of covariance (ANCOVA—Sokal and Rohlf, 1981) using GLIM software (Francis et al., 1993). We then tested for an effect of cohort on first-annual increment with an analysis of variance (ANOVA—Sokal and Rohlf, 1981). Next, we replaced cohort effects by meteorological variables and performed a stepwise multiple regression with backward elimination (Searle, 1971). Testing several variables in a single model increases the risk of type I errors. To control for this kind of error, we used the C_p of Mallows (Mallows, 1973) for model selection (Burnham and Anderson, 1992). To test if ibex showed compensatory horn growth after 1 year of age, we tested for a correlation between adult horn length and first-annual increment, after the effect of age was removed. For this analysis, we first performed a regression of adult horn length on log-transformed age and then correlated standardized residuals from this regression with first-annual increment (using STATVIEW-II software—Feldman et al., 1987).

Results

We used measurements of 100 males aged 1–12 years at capture, 48 females aged 1–14 years at capture, and 36 females aged 1–4 years at capture. Age and cohort had additive effects on chest girth of males (age effect: $F = 404.62$; $d.f. = 1, 83$; $P < 0.0001$; cohort effect: $F = 2.08$; $d.f. = 11, 83$; $P = 0.03$), but only age affected chest girth among females ($F = 14.85$; $d.f. = 1, 35$; $P < 0.0001$; Fig. 1). We obtained the same results with the sample of females aged between 1 and 4 at capture ($F = 42.04$; $d.f. = 1, 33$; $P < 0.0001$). Only April snow depth had a significant, negative, effect on male chest girth ($F = 4.91$; $d.f. = 1, 90$; $P = 0.029$; Table 1). As snow depth in April increased, chest girth of males at a given age decreased. As expected from the absence of cohort effects among females, climatic variables had no effect on chest girth (Table 1).

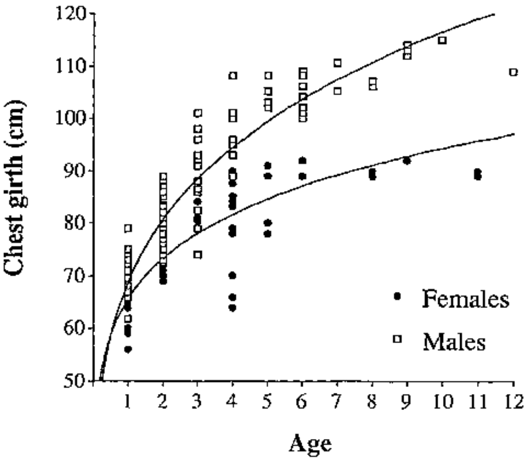

FIG. 1.—Relationship of girth and age of male and female ibex in Belledone, France.

First-annual increment was more variable for males than females, all cohorts being pooled together (variances of 11.83 and 3.72, respectively, $F = 3.18$; $d.f. = 98, 32$; $P < 0.0001$; Fig. 2). Adult horn length did not vary among cohorts but increased with age in males ($F = 296.72$; $d.f. = 1, 70$; $P < 0.0001$; Fig. 3) and females ($F = 41.75$; $d.f. = 1, 22$; $P < 0.0001$; Fig. 3). On the other hand, the first-annual increment of male horns varied among cohorts ($F = 2.90$; $d.f. = 5, 43$; $P = 0.024$), but not of females ($F = 0.43$; $d.f. = 11, 22$; $P = 0.925$). When we replaced cohort by meteorological variables, only spring temperature accounted for a significant part ($r^2 = 0.17$) of yearly variation in first-annual increment of male horns ($F = 5.971$; $d.f. = 1, 65$; $P = 0.017$). First-annual increment of males was correlated negatively with spring temperature (Fig. 4). Climatic variables had no effect on the first-annual increment among females (Table 1).

Standardized residuals of the regression of adult horn length on age were correlated

TABLE 1.—*C_p (Mallows, 1973) for the multiple regression of chest girth and first-annual increment of horns with climatic variables for male and female alpine ibex in Belledonne, France. Models worse than the complete model (indicating a significant effect of the tested variable) are coded with an asterisk (*). For females, results of the analyses using all females and using only females aged 1–4 years at capture are given.*

		Model				
Measurement	Sex	Complete	Without spring temperature	Without spring precipitation	Without winter snow-depth	Without April snow-depth
Chest girth	Male	6.00	4.65	4.94	4.28	8.90*
	Female	6.00	4.01	4.205	4.03	5.36
	Female (1–4)	6.00	4.00	4.01	4.15	4.03
First increment of horn	Male	5.00	9.33*	3.43	3.04	3.97
	Female	5.00	4.90	3.09	3.42	3.07

inversely with first-annual increment for 24 females (r^2 = 0.363; *d.f.* = 1, 22; P = 0.002) but not for 53 males (r^2 = 0.019; *d.f.* = 1, 53; P = 0.328; Fig. 5). Females apparently compensated for a small first-year horn growth.

DISCUSSION

We detected long-term cohort effects on male but not female adult body condition. This result suggests that both food availability and selection on differential maternal care according to sex are likely to play a role in the presence (or absence) of long-term cohort effects. Indeed, the ibex population we studied was young, and available data indicate that it was not resource-limited. Adult survival was high (0.97), constant over time, and similar for males and females (Toïgo et al., 1997). Population growth rate was high (Toïgo et al., 1996), and reproductive success of adult females also was high (J. Michallet, in litt.). Consequently, individuals should have been able to compensate for early growth dis-

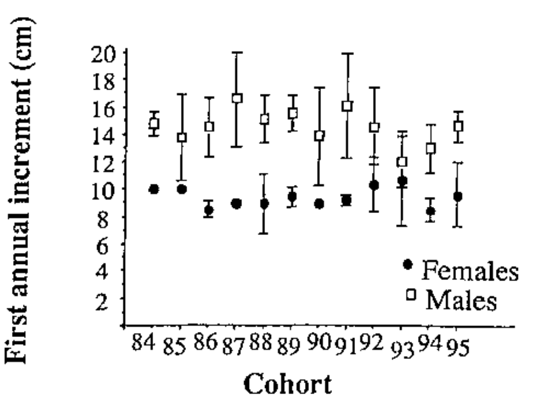

FIG. 2.—Length of first-annual increment of horns of male and female ibex in Belledone, France. Standard error is represented by the vertical bars.

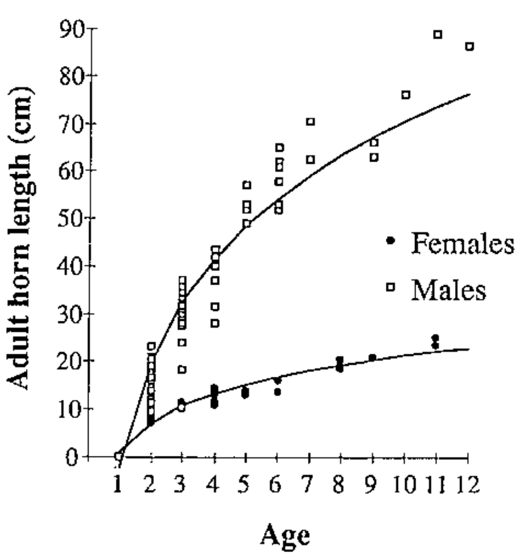

FIG. 3.—Relationship of adult horn length (total horn length minus first-annual increment) and age of male and female ibex in Belledone, France.

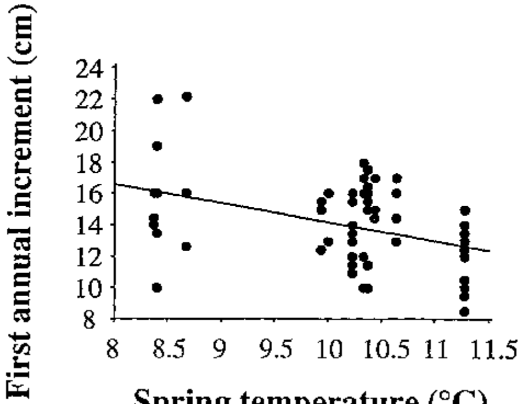

FIG. 4.—Relationship between first-annual increment of male ibex and spring temperature in Belledone, France.

advantages. Our analyses on female growth fit these expectations. Thus, the abundant food supply in the study area apparently allowed compensatory growth to occur in females. However, despite abundance of food resources, males with low early growth were not able to catch up to males with high early growth, even in adulthood. Thus, evolutionary constraints may act on males to prevent compensatory growth. These constraints may have evolved because of male-biased maternal care and polygyny of ibex. Indeed, observations conducted during 3 consecutive breeding periods on suckling behavior suggested that females tend to provide more maternal care to sons than daughters (Toïgo, 1998). On the other hand, ibex have a tending mating system, with a high level of polygyny for dominant males (Couturier, 1962). If mothers tend to provide extra maternal care to their sons to increase their inclusive fitness, then early maternal care is likely to be related to adult body size.

Effect of mean snow cover in April on male chest girth suggests that duration of winter preceding birth may have a delayed effect on males by affecting condition of the mother. During late gestation and early lactation, energy requirements of mothers are largely increased (Oftedal, 1984; Robbins and Robbins, 1979), and several studies have shown that maternal body condition during those phases had an important impact on birth weight and neonatal growth rate of young (Gaillard et al., 1993*a*; Robertson et al., 1992; Verme, 1963) or milk availability (Festa-Bianchet, 1988; Langenau and Lerg, 1976). In temperate areas, maternal body condition has been shown to be related to environmental conditions that affected food availability preceding parturition (Langenau and Lerg, 1976; Robertson et al., 1992; Verme, 1963). If winter is long, loss in female body mass will be greater, and mothers will not obtain enough available resources to replenish their forces be-

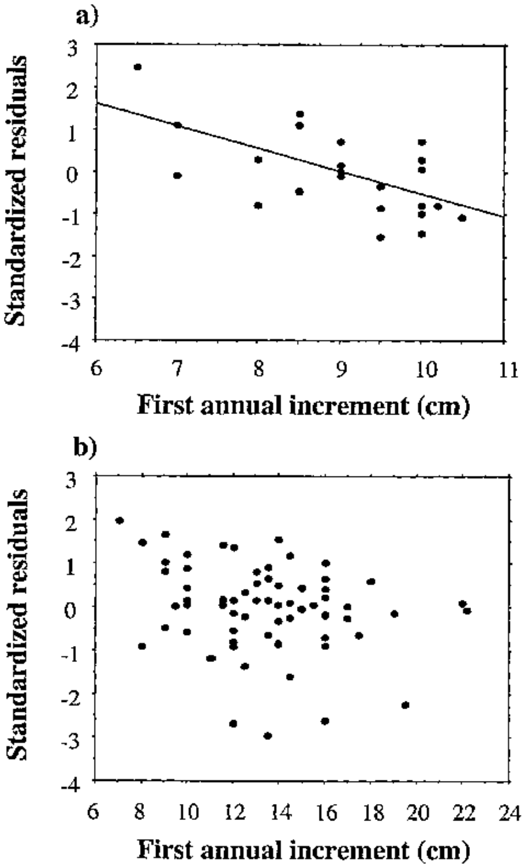

FIG. 5.—Relationship between standardized residuals of the regression of adult horn length (total horn length minus first-annual increment) on age and first-annual increment for female a) and male b) ibex in Belledone, France.

fore parturition. Mothers in poor body condition will give birth to lighter young and will produce less milk, leading to a slower juvenile growth rate and so a lower body weight at 1 year of age. After this age, small males will have the same growth rates as males of other cohorts; they will not compensate for their lighter juvenile body weight and will remain relatively small. Contrary to males, females will be able to compensate for delayed growth.

In contrast to chest growth rate, male first-annual increment was not affected by winter conditions but by spring temperature. Surprisingly, the correlation between first-annual increment and spring temperature was negative, whereas a positive relationship usually relates spring temperature to plant quality and quantity (Brühlman and Thomek, 1991; Dietl, 1979). In our study, it seems that food resources available for ibex are less abundant when climatic conditions favor vegetation growth. Our study area was used by flocks of domestic sheep. When spring temperature is low, snow cover in the areas occupied by ibex during late spring and early summer is greater, leading sheep to use habitats situated at a low elevation (with less snow cover), where they do not compete with ibex. Spring temperature influenced horn growth of males only. Two non-exclusive hypotheses could account for this result. First, the extent of extramaternal care toward sons could be limited by environmental conditions (Pélabon et al., 1995). Second, horns may have evolved different function in males and females. Female horns may have evolved as antipredator weaponry to protect young (Geist, 1966), whereas male horns may have evolved under sexual selection. Male horns are indeed considered to be very important for reproductive success in sexually dimorphic ungulates like ibex (Clutton-Brock et al., 1982; Geist, 1974). Secondary sexual characters are subject to higher variability due to environmental constraints. When food resources available are scarce or of low quality, male ibex may reduce energy allocated to horn growth to maintain a high body growth rate, and thus increase the probability of surviving during the 1st winter.

Acknowledgments

We are grateful to Office National de la Chasse, and more specifically to M. Catusse, D. Dubray, L. Ellison, and Y. Tachker, who permitted the study. We also thank all persons who contributed to data collection, and we are more specifically grateful to D. Blanc for his helpful monitoring of the reserve. We thank M. Boyce, C. Pélabon, D. Pontier, E. Verrier and N. G. Yoccoz for constructive comments on previous drafts of this manuscript.

Literature Cited

Albon, S. D., T. H. Clutton-Brock, and F. E. Guinness. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. The Journal of Animal Ecology, 56:69–81.

Albon, S. D., T. H. Clutton-Brock, and R. Langvatn. 1992. Cohort variation in reproduction and survival:implications for population demography. Pp. 15–21, *in* The biology of deer (R. D. Brown, ed.) . Springer-Verlag, New York.

Andersen, A., and J. D. C. Linnell. 1997. Variation in maternal care in a small cervid; the effects of cohort, sex, litter size and time of birth in roe deer (*Capreolus capreolus*) fawns. Oecologia, 109:74–79.

Brühlman, M., and P. Thomek. 1991. Verlauf des quantitativen und qualitativen futterangebotes auf Alpweiden. Landwirtschaft Schweiz, 4:547–554.

Bunnell, F. L. 1978. Horn growth and population quality in Dall sheep. The Journal of Wildlife Management, 42:764–775.

Burnham, K. P., and D. R. Anderson. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pp. 16–30, *in* Wildlife 2001:populations (D. R. McCullough and R. H. Barrett, eds.) . Elsevier Science Publishers, Ltd., Oxford, United Kingdom.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: Behavior and ecology of two sexes. The University of Chicago Press, Chicago, Illinois.

Couturier, A. M. J. 1962. Le bouquetin des Alpes. Arthaud, Grenoble, France.

Dietl, W. 1979. Standortgemässe verbesserung und bewirtschaftung von Alpweiden. Tierhaltung, 7. Birkhaüser verlag, Stuttgart, Germany.

Feldman, D. S., R. Hofman, J. Gagnon, and J. Simpson. 1987. Statview II. La solution pour l'analyse de données et la représentation graphique. Abacus Concepts Inc., Berkeley, California.

FESTA-BIANCHET, M. 1988. Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birth date and sex. Animal Behaviour, 36:1445–1454.

FESTA-BIANCHET, M., J. T. JORGENSON, AND W. D. WISHART. 1994. Early weaning in bighorn sheep, *Ovis canadensis,* affects growth of males but not of females. Behavioral Ecology, 6:21–27.

FRANCIS, B., M. GREEN, AND M. PAYNE. 1993. The GLIM system. Release 4 manual. Clarendon Press, Oxford, United Kingdom.

GAILLARD, J.-M., D. DELORME, AND J.-M. JULLIEN. 1993*a*. Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. Oecologia, 94:57–61.

———. 1993*b*. Croissance précoce et poids à l'entrée de l'hiver chez le faon de chevreuil (*Capreolus capreolus*). Mammalia, 57:359–366.

GAILLARD, J.-M., J.-M. BOUTIN, D. DELORME, G. VAN LAERE, P. DUNCAN, AND J.-D. LEBRETON. 1997. Early survival in roe deer: causes and consequences of cohort variation in two constrasted populations. Oecologia, 112:502–513.

GEIST, V. 1966. The evolutionary significance of mountain sheep horns. Evolution, 20:558–566.

———. 1974. On the relationship of ecology and behaviour in the evolution of ungulates:theoretical considerations. Pp. 235–246, *in* The behavior of ungulates and its relation to management (V. Geist and F. Walther, eds.) . I.U.C.N. Publications, New Series.

HEWISON, A. J. M., AND J.-M. GAILLARD. 1996. Birth sex ratios and local resource competition in roe deer, *Capreolus capreolus*. Behavioral Ecology, 7:461–464.

KREBS, C. J., AND I. MC. COWAN. 1962. Growth studies of reindeer fawns. Canadian Journal of Zoology, 40: 863–869.

LANGENAU, E. E., AND J. M. LERG. 1976. The effects of winter nutritional stress on maternal neonatal behaviour in penned white-tailed deer. Applied Animal Ethology, 2:207–223.

MALLOWS, C. L. 1973. Some comments on C_p. Technometrics, 15:661–675.

MAYNARD-SMITH, J. 1980. A new theory of sexual investment. Behavioral Ecology and Sociobiology, 7: 247–251.

MICHALLET, J., B. GRAND, AND J. BONARDI. 1988. La population de bouquetin des Alpes de la réserve de Belledonne-Sept-Laux. Bulletin Mensuel de l'Office National de la Chasse, 125:19–24.

OFTEDAL, O. T. 1984. Body size and reproductive strategy as correlates of milk energy output in lactating mammals. Acta Zoologica Fennica, 171:183–186.

PÉLABON, C. 1997. Is weight at birth a good predictor of weight in winter for fallow deer? Journal of Mammalogy, 78:48–54.

PÉLABON, C., J.-M. GAILLARD, A. LOISON, AND C. PORTIER. 1995. Is sex-biased maternal care limited by total maternal expenditure in polygynous ungulates? Behavioral Ecology and Sociobiology, 37:311–319.

ROBBINS, C. H., AND B. L. ROBBINS. 1979. Fetal and neonatal growth patterns and maternal reproductive efforts in ungulates and subungulates. The American Naturalist, 114:101–116.

ROBERTSON, A., M. HIRAIWA-HASEGAWA, S. D. ALBON, AND T. H. CLUTTON-BROCK. 1992. Early growth and suckling behaviour in Soay sheep in a fluctuating population. Journal of Zoology (London), 227:661–671.

SEARLE, S. R. 1971. Linear models. John Wiley & Sons, New York.

SHULTZ, S. R., AND M. K. JOHNSON. 1995. Effects of birth date and body mass at birth on adult body mass of white-tailed deer. Journal of Mammalogy, 76: 575–579.

SOKAL, R. R., AND R. J. ROHLF. 1981. Biometry: the principles and practice of statistics in biological research. Second ed. W. H. Freeman and Company, San Francisco, California.

TOÏGO, C. 1998. Stratégies biodémographiques et sélection sexuelle chez le bouquetin des Alpes (*Capra ibex ibex*). Thèse de doctorat, Université Claude Bernard, Lyon1.

TOÏGO, C., J.-M. GAILLARD, AND J. MICHALLET. 1996. La taille des groupes: un bioindicateur de l'effectif des populations de bouquetin des Alpes (*Capra ibex ibex*)? Mammalia, 60:463–472.

———. 1997. Adult survival in the sexually dimorphic alpine ibex (*Capra ibex ibex*). Canadian Journal of Zoology, 75:75–79.

TRIVERS, R. L., AND D. E. WILLARD. 1973. Natural selection of parental ability to vary sex ratio of offspring. Science, 179:90–92.

VERME, L. J. 1963. Effect of nutrition on growth of white-tailed deer fawns. Transactions of North American Wildlife and Natural Resources Conference, 24:431–443.

———. 1983. Sex ratio variation in *Odocoileus*:a critical review. The Journal of Wildlife Management, 47:573–582.

Submitted 24 November 1997. Accepted 28 September 1998.

Associate Editor was John A. Litvaitis.